THE FARMER AND STOCK-BREEDER MANUALS

GENERAL EDITOR: HAROLD C. LONG, B.Sc. (EDIN.)
Ministry of Agriculture and Fisheries

CROP AND STOCK IMPROVEMENT

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The volumes in this series have been planned with *The Farmer and Stock-Breeder* in order to place at the disposal of practical farmers and those who intend to take up agriculture as a profession a summary of the broad scientific principles governing farming on a business basis, and, at the same time, to embody such notes as are necessary to enable these principles to be applied from day to day.

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PREFACE

THE volumes in this series are intended to place at the disposal of practical farmers and those who intend to take up agriculture as a profession a summary of the broad scientific principles governing farming on a business basis, and, at the same time, to embody such notes as are necessary to enable these principles to be applied from day to day.

With this object the Manuals have been written as far as possible in non-technical language, and, in order that they may be available at a reasonable price and in a convenient form, all unnecessary detail has been omitted.

It is often made a reproach against scientists, and particularly scientists whose province is Agriculture, that they do not take sufficient pains to explain what they are doing, and why they are doing it. The Farmer and Stock-Breeder Manuals have been planned specifically to answer this charge and make available to practical farmers the results of the best scientific thinking and research. In a few cases the principles laid down may be contrary to current practice, but it should be realized that this fact is in reality a testimony to the value of the series. What is new in scientific farming is not only a question of words but a question of ideas. Ideas divorced from practical experience are of little value, but nothing will be put forward in these Manuals which has not been tested in practice.

H. C. LONG.

September 1926

AUTHORS' PREFACE

THE authors are fully conscious of the inadequacy of treatment which considerations of space have forced upon them in writing this little book. They would ask readers to remember that the main object is, firstly, to explain and, secondly, to illustrate the *principles*—and more especially the scientific principles—of improvement. An attempt will be made to show that in recent years great progress has been made in ascertaining and defining the *laws* of heredity, and that in relation to the breeding of plants scientific improvers have achieved a number of notable successes. On the other hand, it is pointed out that, owing mainly to the costliness and time-consuming nature of experiments with animals, knowledge gained from actual experiment is still somewhat defective, but enough has been learned to define with some confidence the lines upon which progress in animal improvement should proceed.

It must be clearly realized that the modern science of Genetics does not claim to have discovered much that is entirely new; in fact the claim is rather that laws have been substituted for a mass of uncoördinated empirical knowledge, and that, consequently, the process of improvement having been made systematic, progress is more rapid, and ultimate success is more likely.

Scientists are fully conscious that much remains to be learned. They would be much assisted and encouraged if workers who have to grapple with breeding problems in the course of their business, or profession, would experiment, or, at least, apply the new knowledge to these problems, and thus satisfy themselves as to its value.

It may be confidently expected that they would add

greatly to the body of accurate knowledge on the subject, and at the same time benefit their business.

In writing this book, the authors have endeavoured to present this new knowledge in as simple language as possible for the benefit of those readers who may not be familiar with scientific ideas and expressions. They are conscious that in doing so they may have sacrificed in some cases that accuracy of definition and expression which the exposition of science rightly demands. For that defect, and no doubt many others, they trust they will be pardoned.

A. B. B.
H. H.

September 1926

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CHAPTER I

INTRODUCTION

THE art of improving plants and animals is one of the most ancient practised by man; his achievements have been so fundamental that they lie at the root of civilized life, but the science of breeding improved plants and animals, which it is the purpose of this book to illustrate and explain, began only with the present century. The art owes its value to the slow-bought knowledge of centuries of experience; the science of breeding, on the other hand, has achieved its results by the application of the knowledge gained from modern scientific observation and experiment. Experience unenlightened by science has almost ceased to add to knowledge; but we have only touched the fringe of scientific discovery. Upon the judicious combination of art with science all progress in husbandry depends.

Even before man became a tiller of the soil and learned the art of husbandry he must have practised the improvement of animals. As a savage he was a hunter: it must have been mainly for the purpose of capturing animals to serve as food that the improvement of the dog was undertaken; and if, as Darwin believed, the domestic dog is descended from the wolf and jackal, no more significant example of man's power of improving the appearance and character of animals can be found. Again, man, the tiller of the soil, produced the ox, and, as a hunter, no doubt the horse: neither is found in a wild condition at the present day. Then the cereals must be improvements of forms which at one time were grasses: a wild form of wheat still grows in Palestine, and all are familiar with wild barley

and oats, which, if not the parents of, must be closely allied with, the domestic species of these plants.

There is no mystery about the methods employed in breeding improved animals and plants. Animals have been improved by cross-breeding and selection, plants originally by selection alone; it is only recently that the improvement of plants by hybridization has been undertaken. In following these processes during the course of centuries, a mass of knowledge and skill has been gained ; and in general practice the skilled stock-breeder of to-day, particularly in Britain, has little to learn ; he must admit, however, that the element of luck enters largely into all breeding operations with animals.

Knowledge of principles, science, has enabled man to add continually to his victories over nature. To mention the most recent of these in the material world, he has learned to fly, and to transmit the human voice from England to the Antipodes through the air. In both these instances theory and scientific study preceded practice. That similar victories have been won by the same means in the improvement of living things it is our hope to show in the following pages.

As has been said, the production of an improved plant or animal has been hitherto largely a case of hit or miss. We have been ignorant of the precise manner in which nature's machine works, and our power of control has consequently been limited. During the last quarter of a century, however, we have added to our knowledge: heredity is losing some of its obscurity, and we are beginning to see that, although much mystery still remains, nature works upon a number of limited principles, and that *if we understand these principles* we can make use of

them in order to attain a desired result. In a sense, it is now possible to "make" improved plants; new wheats, barleys and oats well known to practical men have already been "made"—that is, built up on a definite plan by a series of steps each of which is under control, just as, let us say, in building a motor-car each part is constructed separately to take its appointed place in the finished vehicle. Scientific study has revealed many, though not all, of the principles which govern the operation of heredity. Law and order have been substituted for many of the chance operations of the breeder. Even from a business standpoint it should be to the advantage of practical men to know what these principles are; if they only occasionally assist his practice, at least they will add to its interest and fascination.

Before embarking upon our task it is important to emphasize, at the outset, that it is not possible to grasp the significance of the new knowledge that is now available unless a clear conception is gained of certain facts and ideas which, although they are familiar to scientists, are not commonly known by everyday men.

We are concerned, then, in the main, with the laws of heredity—that is, the rules regulating the transference of the characters of a plant or animal to its offspring. The most outstanding fact in this transference is that while, as a general rule, "like begets like," all improvement is based upon the fact that *like sometimes produces unlike*; and it is by seizing on the unlike, in the hope of perpetuating the new qualities or characters, that all progress depends. Now the new knowledge enables the scientist in many cases not only to predict the occurrence of unlike offspring, but also to indicate how the new characters may be fixed, if so desired.

The next fact to be noted is that this unlikeness is most readily produced by bringing together the male and female elements of individuals with diverse characters. Male and female elements are separable in plants as well as in animals; just as an animal is produced from the union of one sperm cell of the male with one egg cell of the female, so the seed of a plant arises from the union of a pollen cell (male) with the egg cell (female). In the individual resulting from this union there is generally a mixture of the characteristics of the two parents. Recent investigations enable the scientist to predict the constitution of this admixture, and to indicate the extent to which the new combination will persist in succeeding generations.

The third, and perhaps the most significant, advance in knowledge is the recognition of the fact in relation to heredity, that many of the various characters of an individual may behave as separable units, so that the offspring of the union of male and female (whether in plants or animals) is not necessarily a union of *all* the characters of the two parents, but rather a reshuffle, in process of which some characters may drop out altogether in the make-up of any one individual. Moreover, the rearrangement takes place in obedience to definite and well-ascertained laws. For example, it is now known definitely that if the child of a brown-eyed father and a blue-eyed mother has blue eyes, the substance, whatever it may be, which produces the brown eyes is absent in that particular child (it may of course be present in other children of the same union); and further, it is possible to assert definitely that the offspring of that child will not revert to the brown eyes of their grandfather. This fact illustrates the principles of separable unit characters, and, together with a large array

of similar facts and the deductions from them, lies at the root of the application of scientific principles to plant and animal breeding: it is known as "the principle of unit characters."

In the pages that follow, many examples will be given which will make the operations of this law clear, but the reader must, we repeat, have a clear grasp of its meaning and implications, for it involves a new departure in conceptions of heredity. Hitherto we have been accustomed to assume that, necessarily, *something* of *all* characters of an individual passes to his descendants, and that, at any time afterwards, any particular character might "revert" to the condition in which it was observed in an ancestor. Now we know that this is not so: some characters disappear altogether from some of the progeny in the first generation; others, it is true, may be present but not apparent for many generations. The important new fact is that in many cases we know the laws which regulate these appearances and disappearances, and can make use of them so as entirely to obviate reversion. The individual, therefore, can no longer be regarded as an indivisible unit.

For the purposes of heredity the individual must be regarded rather as a colony of unit characters each of which may, and often must, go separate ways in the offspring of that individual. Also, it must be clearly understood that this is no "theory"; a multitude of facts, which is being added to every day, proves the truth of this assertion. If further evidence be needed we have only to point to the successes that have already been achieved. "Yeoman" wheat and "Spratt-Archer" barley were both produced (and could not have been produced otherwise) by the application of the principle we have just endeavoured to explain. "Reversion" has ceased to be a mysterious

principle of nature, obeying no known law; it is something that can be explained when it occurs, and can often be predicted with the same certainty with which an astronomer predicts an eclipse of the sun years before its occurrence.

Finally, attention must be drawn to a principle which dominates all scientific work on breeding; it is one to which, it is thought, practical breeders might give greater attention. Shortly stated it is this. The study of progeny is of greater importance and more fruitful than the study of pedigree. The value of the latter must be recognized, but the acid test of pedigree is performance. It will be admitted readily that a parent belonging to pedigree stock does not always get progeny of a satisfactory standard. This is particularly marked in the case of bulls with a milk pedigree; the performance of their daughters is often mediocre. Yet a pedigree animal may often be described as "pre-potent": in other words, it has the power of transmitting its good qualities to its offspring, and the more "pre-potent" he is the higher his merit. It may be said therefore, with confidence, that offspring provide a better criterion of the merits of an individual for breeding purposes than pedigree; at any rate the advances that have been made in breeding improved plants owe their origin to the application of laws which have been derived from the study of progeny rather than pedigree.

It is not pretended that all operations of heredity can be explained or controlled; much still remains to be learned. Nevertheless, as we shall see, law and order prevail in regard to many of the appearances which have hitherto been considered mysterious and incapable of control.

In the following pages the improvement of plants will

be considered separately from that of animals, but, so far as the ascertained laws of heredity are concerned, the significant principles are believed to be the same. The practical successes obtained in improving plants, however, have so far been greater than in the case of animals, and deserve earlier consideration.

CHAPTER II

IMPROVEMENT OF PLANTS BY SELECTION

In the opening chapter it was stated that the domestication of various wild plants ultimately led, through selection, to the plants of economic value which we now possess. Use was made of the fact that "like" does not always "produce like." As an exception to the rule, "unlike" is occasionally produced, and it was by seizing on the unlike offspring of wild plants that our forefathers ultimately produced the crop-bearing plants. As a matter of fact, no single offspring of either a plant or an animal is precisely like its parent, or parents. There is always some variation, however minute, and further, it seems to be the fact that, under domestication, this tendency to vary is intensified. It may be recalled that a careful study of the variation of animals and plants under domestication led Darwin to his celebrated theory of the Origin of Species. He believed that nature exercised a selective influence, and that variations (which, be it noted, he assumed were *all* inherited) by a cumulative action eventually produced all the differences between animals and plants which we now observe in nature.

Two Forms of Selection.—There can, consequently, be no doubt that continued selection in a desired direction does ultimately lead to improvement. Scientists, however, recognize two forms of variation. One is termed "fluctuation," the other "mutation." These terms mean simply that some variations are inheritable, others are not, and that the selection of the latter is without effect. Generally speaking, minute quantitative variations are not inherited; they simply represent the changes which differing environment

bring about. Of these, by far the most important are the variations resulting from the changes in the environment of the mother plant or animal. Everyone recognizes that the quality of seed barley, for example, is influenced by the soil and season which the mother seed plant experiences; and the vigour of, say, a calf depends, to some extent, on the health and vigour of the cow in whose womb it spent the first nine months of its existence.

Now, scientists believe that the selection of these casual (environmental) fluctuations does not result in improvement, but that variations of the other kind, mutations, are caused by fundamental differences in breed, present at birth. The latter are *qualitative*; they may be as minute as the other, such as differences in the "breed" of barley in respect of malting quality, but they are nevertheless profoundly different—they are heritable. How and why they arise we do not know. The value of selection, it is believed, depends wholly upon the occasional presence of these heritable variations (for non-heritable fluctuations are the commoner). Selection is effectual only in so far as it results in the perpetuation and multiplication of these mutations. The practical result, therefore, is that selection practised without any discrimination, while it may be, and in the long run generally is, effective, is often an unnecessary waste of time; whereas, if carefully guided, the process becomes systematic and leads to great saving of time. Modern plant improvement by selection has adopted the practice of starting the process with a single plant: there are sound scientific reasons for doing so, firmly based on what are now known as the Laws of Heredity. These reasons we hope to explain. As a preliminary, it will be

well to consider what we know historically regarding plant improvement by selection.

Historical.—In Europe the earliest precise records of crop improvement are those furnished by the classical writers, who record that in choosing seed their husbandmen were influenced not only by the district from which it was obtained, but also by its size. There are, for instance, repeated admonitions in various Roman and other early writers not to use seed from cold, wet land, to use that from drier soils, and to reserve from the threshed crop the largest and best-filled grains. A further opinion one finds expressed is that if a choice of ears is made, the grain from those exhibiting freedom from gaps, or, as the botanist now expresses it, infertile florets, should alone be retained for seed. Improvement based on these maxims alone was necessarily very slow.

In the British Isles early development of scientific crop improvement is associated with the work of three investigators: Patrick Shirreff, Colonel Le Couteur (1820) and Major Hallett (1860); and it is noteworthy that the methods of procedure adopted by the two former are in the main identical with those largely practised by the pure selectionist to-day.

Patrick Shirreff, a Haddingtonshire farmer, may rightly be regarded as a pioneer of systematic crop improvement. His method of procedure was as follows:—Struck by the more vigorous appearance of certain individual plants in his crop of wheat and oats, he took steps to secure such plants against accidental damage, and when they were fully ripe harvested them *separately*, threshed them out with the greatest care to avoid admixture with grain from other plants, and sowed the seed in plots in succeeding

years until he secured a sufficient quantity to place the product on the market.

The first of Shirreff's selections, a variety of wheat known as "Mungoswell," appeared in 1825. It was obtained from a plant which attracted Shirreff's notice in the spring of 1819 growing luxuriantly in a field of wheat "then looking miserable from the effects of a severe winter." [1]

Similarly, in the summer of 1824, Shirreff noticed *one* tall oat plant growing in a crop of this cereal, saved the grain therefrom and sowed it in the following spring in competition with several other varieties. At harvest the plants from this selection proved the tallest of the series and at least six to eight inches taller than Potato oat. It was, ultimately, introduced to the public under the name of Hopetoun Oat. Subsequently, he introduced the "Fellow" family of oats, "Fine Fellow" and others—all raised from single plants distinguished by the adoption of the same practice—single plant selection.

Colonel Le Couteur's work on cereals is remarkable, not only by reason of its actual achievements, but also because he received his first stimulus from a chance observation of a stranger on a fact which is the basis of crop improvement. Professor Mariano Lagasca of Madrid, whilst on a visit to Le Couteur at his farm in Jersey, pointed out to his host the mixed condition of his fields of wheat, and suggested that some of the component plants, if grown on singly, might be more productive than others. Acting on this suggestion, Le Couteur saved a number of single plants, and cultivated the produce of each separately

[1] Patrick Shirreff: *Improvement of the Cereals.* William Blackwood & Sons, 1873.

until he could compare their value. In 1830 he placed one named "Talavera de Bellevue" on the market, and this is still a highly prized wheat in France.

Major F. F. Hallett of Brighton worked on an entirely different principle to Shirreff and Le Couteur. His efforts were confined to an attempt to effect an improvement within the produce of a single selected plant by choosing yearly for further propagation the best grains from the best ears. It is probably right to say that, in so far as Hallett selected fluctuating variations, he failed to secure any improvement; whereas, if he by chance lighted on mutations (and it is doubtful whether he did), improvement resulted.

Self-fertilization and Cross-fertilization.—To make the position with regard to selection quite clear it is necessary to state at the outset that, in considering the question of propagating selected individuals, plants may be divided into two classes: those which are self-fertilizing, and those which are commonly and normally fertilized with pollen from other plants of the same species. In plants, as in animals, there are male and female organs. In plants the ovary, or female organ, is contained in the flower, generally surrounded by other floral organs described as the petals and sepals, the former being frequently bright coloured. The male organs, or stamens, may exist separately, or, more commonly, are contained within the flower together with the ovary. The stamens, when ripe, readily discharge their contents, which consist of a large number of small pollen grains. The top of the ovary is usually developed into processes termed stigmas, which are of such a character as to retain pollen grains falling or being shed upon them. The surfaces of the stigmas sometimes give off a sticky liquid or

take the form of small feathery branches capable of catching and retaining pollen grains as they are shed from the stamens. Once on the stigma the pollen grains germinate and send a fine tube down between the cells of the stigma into the ovary. Here a fusion of the nucleus of the ovary and that of the pollen grain takes place, and the resulting body, after repeated divisions, slowly develops into a seed.

The three cereals, wheat, barley and oats, and most leguminous crops, such as peas and beans, are self-fertilizing under normal conditions, whilst clovers, grasses and root crops in some cases require pollen from other plants to fertilize them : clovers are actually self-sterile, their own pollen being ineffective. In self-fertilizing plants the pollen of each flower is capable of fertilizing the ovule of the same flower, so that the crop is subjected to a continued process of in-breeding. As we shall show later, the ultimate result is to fix the type; germinal variation (mutation) practically entirely disappears. The offspring of each plant is an exact replica of its parent, so far, at least, as internal composition is concerned.

Pure Line and Mass Selection.—Professor Johannsen of Copenhagen applied the term "pure line" to the progeny of continually self-fertilized plants originating from one mother plant. The question which he set himself to solve was: Can we, by repeatedly selecting extreme fluctuations in the produce of a pure line, through many generations, obtain a definite and heritable improvement in any desired direction? Concretely, starting with a single plant of wheat, barley or oats, can we, by selecting the largest grains produced through a number of years, increase the average size of grain of that particular selection?

Professor Johannsen carried out his investigations with barley and kidney beans, using infertility (non-setting of grain) in the former and the weight of seeds in the latter as subjects for observation. In the case of the beans he began by choosing from an ordinary commercial bulk of kidney beans a series of seeds differing in individual weights. These were sown under carefully regulated and comparable conditions, and, when fully ripe, the seeds obtained from each original bean were weighed. Professor Johannsen then found that even in the case of the produce of each single plant there was always a considerable variation in size, some beans being large, others distinctly small, and a large number of sizes intermediate between these two. He calculated the mean weight of beans in the produce of each plant and in succeeding years continued to weigh the produce from each bean that he sowed. The conclusions finally arrived at were that each of the original beans sown was capable of producing beans of a certain definite mean weight, some being high, some low and some intermediate. Moreover, if he took a large bean of any one line, or, similarly, a small one of the same line, the beans he obtained therefrom were not large in the case of the large parent, or small in that of the small; they were large, small and intermediate in both cases, with the same average as that previously determined for that particular line. Thus, the original commercial sample could be regarded as consisting of a large number of individual lines each capable of producing progeny characterized by a definite average weight. To an indiscriminate collection of lines of this description Professor Johannsen applied the term "population." A large bean picked out of such a population at random would not necessarily produce large beans again; for it might

prove to be either a large individual seed of a line with a low mean weight, or it might be a small bean of a line with high average weight.

It is desirable to contrast, briefly, a third system of improvement, that of mass selection. The basis of mass selection is the choice from a field of an unselected crop, or, to use Johannsen's words, "population," of all the plants exhibiting the highest development of the desired characters. This system had several well-known exponents, prominent amongst whom was J. Rimpau, who developed the famous Schlanstedt variety of rye. The seed from selected rye plants was sown as one bulk, and a further selection was made in the produce obtained therefrom. As a result of the continued repetition of this procedure, through a series of generations, a collection of forms was ultimately arrived at, which represented a close approximation to the form the breeder had in view. Once the seed got into general circulation, however, and the annual selection ceased, the produce showed a slow but persistent deterioration in evenness and eventually in yield, and the grower was compelled to obtain fresh stocks from the original selector. Another example of mass selection is provided by the activities of the Swedish Seed Association, which, in 1886, began its crop improvement operations at Svalöf in southern Sweden. For several years the workers there attempted by mass selection to produce improved varieties of wheat, barley and oats which would maintain their uniformity and superiority, but without any success. Quite accidentally, however, it was discovered that the produce of *single* plants maintained a marked uniformity, and this fact enabled the Swedish investigators to initiate a series of single-plant, or pure-line, selections that has

raised their productions to a leading position in Europe and other parts of the world.

The most outstanding example of success achieved by mass selection is provided by the history of the improvement of sugar-beet. By repeated selection in the mass of roots of high sugar content, the improvers succeeded, between 1820 and 1900, in raising the average sugar content of the roots from 7-8 to 17-18 per cent. We now know that if the produce of the wild plant (*Beta maritima*) be examined, roots with a percentage as high as 22 will be found. All that the improvers did, therefore, was to increase the proportion of roots exhibiting high sugar content. They did not actually produce a plant richer in sugar.

Unselected crops or "populations" consist of a large number of separate units differing from each other in various ways, some of which are indicated above, and the differences, if heritable, form the material on which the selectionist operates. From various populations he selects individual plants possessing the characters he wishes to perpetuate and grows them as separate units, *but once this is done there is little chance of further improving any particular character.* The general effect of single-plant selection is thus to raise the standard of the variety in one or more directions above that of the population from which the parent single plant was drawn, but nothing new is created, the whole of man's effort being confined to the choice, for specific purposes, of individual forms already in existence.

It is clear, therefore, that mass selection—*i.e.* the picking out of a number of plants showing desirable characters—is unscientific—a waste of time, in fact. Plant improvement

by selection must start with the single plant, as the original parent of a "pure line."

Up to the present we have confined our remarks to a consideration of the botanical and physiological characters of the plant, but it has been found that the various lines of which population are composed differ also in characters with a more direct economic bearing, such as the quality and yield of grain. The latter term requires no explanation, but the former has a separate meaning for every crop. Thus in wheat it is usually synonymous with a high total nitrogen or protein content; in barley, with a low albuminoid content; in oats, with low husk and high albuminoid and oil content; in sugar-beet, with high sugar content; in turnips and mangolds with high dry matter, and so on. The occurrence of lines with hereditary differences of this nature, in addition to those already mentioned, increases the chances of improvement in all directions, and the advances that have been made as a result of these ascertained facts have been remarkable when viewed in the light of the position of even thirty years ago. We hope later to give a short summary of some of these achievements.

The method of pure-line selection has in recent years been pursued by plant breeders in India with significant success. When they started work in 1900 (to the late Lord Curzon must be ascribed the credit of initiating the work) they found that the crops of that country consisted of, what Johannsen would term, populations of pure lines. By applying the method of single-plant selection the scientific workers there (of whom Dr and Mrs Howard hold the leading position) have obtained astonishing results. Here are some figures showing the acreage covered by

the improved varieties of crops produced by the scientific plant breeders in India :—

Crop	*Improvement effected*	*Area occupied*, 1923 *Acres*
Wheat	High-yielding, rust-resisting	1,200,000
Cotton	High-yielding	1,500,000
Rice	High-yielding	500,000

So far we have dealt with plants which are ordinarily self-fertilized, for wheat, barley and oats all belong to this class. The pure-line principle, however, applies to cross-fertilized plants, *provided that the access of pollen from other plants can be prevented.* We shall return to the subject in a later chapter.

CHAPTER III

THE HYBRIDIZATION OF PLANTS

In the preceding chapter have been considered the possibilities of selection as a method of crop improvement. It has been shown that the first great step, the domestication of varieties of wild plants for the purpose of food production, was accomplished by selection, most probably by multiplying the offspring of chance "mutations," and by a gradual process of mass selection improving the plant concerned. Precisely how the chance mutations arose we do not know. At the same time it was pointed out that improvement by selection has its limitations. After a certain stage no further advance seems possible. At a comparatively later stage our ancestors awoke to the possibilities of hybridization. This must have been due to the recognition that reproduction in plants is similar to that in animals, in that male and female elements take part. In relation to fruit crops, in particular, hybridization must have been first practised many centuries ago: in no other way can we reasonably account for the number of varieties of fruit-bearing plants, such as the vine and apple, in cultivation from very early times.

Up to as late a period as the end of the nineteenth century, however, improvement by hybridization was a haphazard process: the variations produced seemed to observe no law; their control therefore was impracticable. It is hoped to show in this chapter that the happenings after hybridization do in most cases obey a law, and that, knowing that law, we can make use of it deliberately for the purposes of plant improvement. If improvement in a definite direction is desirable, we can lay down the plan

of operations with the confident anticipation that, if possible at all, the desired end will be attained in that way and no other.

Choice of Variety.—The choice of a variety of any crop for a given set of circumstances is a matter depending upon a combination of a large number of conditions. High yield, whether of grain in cereal crops or of roots in turnips, swedes and mangolds, and of tubers in the case of potatoes, is primarily essential, but this, as it is proposed to show later, must always be viewed in relation to quality as demanded by commercial requirements. Again, some varieties show a preference for certain descriptions of soil and of climate; others are late-ripening, and for this reason unsuitable for conditions where the general tendency is in this direction. In the case of cereals, some varieties are weak-strawed and, consequently, prove unsuitable in circumstances producing great development of straw. Finally, susceptibility to disease may debar the use of a variety, in spite of the fact that all its other characters are desirable.

Early Hybridization not systematic.—Such qualifications render selection for definite conditions a matter of considerable complexity, and frequently the ultimate choice is, at the best, a compromise. These and similar causes led some of the early plant improvers to attempt the production of hybrid plants in the hope of combining in the offspring the good points of two or more parents. In many cases the actual process of artificial hybridization—that is, the transmission of the pollen of one parent to the stigma of the ovary of the other parent—was completely successful, but, in the produce of the hybrid grain, there was in the second and succeeding years a marked and ever-present tendency to what was at that time termed "reversion." None of

the early hybridists appears to have followed the various generations of the hybrid with sufficient attention to enable them to ascertain whether the "reversions" occurred in any definite proportion, nor did they determine which, if any, of the plants of their second generation showed no reversion in the third and subsequent generations. Thus, until about the opening of the present century, the results of plant hybridization were so unsystematic as to limit their use on a larger economic scale. Reversion was regarded as an inevitable and uncontrollable outcome of hybridization, and that it occurred as a characteristic of a portion of the hybrid produce only, was unrealized.

Mendel's Work.—In 1901, however, a translation of Gregor Mendel's (1822-1884) historic paper, "Experiments in Plant Hybridization" (1865), was printed in the *Royal Horticultural Society's Journal*, and in the following year the late Mr W. Bateson published an article on Mendelism, under the title of "Mendel's Principles of Heredity : A Defence." With the appearance of these important publications the study of heredity and the scientific improvement of farm crops and animals received a new stimulus.

Mendel chose the ordinary pea for his experiment in plant hybridization, and selected seven pairs of differentiating [1] characters for observation, but for purposes of

[1] It may be difficult at first to those unaccustomed to studying problems such as we are now dealing with to grasp the full meaning of the word *differentiating*. The essence of Mendel's observations is that plants and animals are built up of a large number of separate characters which, during the process of reproduction, behave as units. Thus if we cross a black and white oat, and decide to follow blackness and whiteness in the progeny of the cross, we can view these as separate characters apart from any other characters of the two parent plants. Both terms, blackness and whiteness, refer to the colour of the grain, which is either one or the other, and hence *differentiating* or contrasting.

illustration it is unnecessary here to mention more than two pairs ; (1) round seeds and angular or deeply wrinkled seeds, and (2) tall and dwarf stems.

On crossing varieties having tall stems with others having dwarf stems, or *vice versa* (Mendel demonstrated that it was immaterial which variety was used as the pollen parent, or which as the seed-bearer), the hybrid plant was always *tall*-stemmed. When the selfed seeds from this tall-stemmed hybrid were sown, some of the resulting plants were tall and others "reverted" to dwarf, but in the definite proportion of *three tall-stemmed plants to one dwarf plant.* Seeds from individual *selfed* plants of both kinds were sown in the third year, and it was then found that those dwarf-stemmed plants of the previous year were *all* dwarf-stemmed. The tall plants behaved differently: of their offspring some were again tall, but others produced tall *and* dwarf plants, in the definite proportion again of three tall plants to one dwarf as in the second year. The proportion of tall plants producing, on selfing, tall plants only, to tall plants producing tall and dwarf plants was 1 : 2, so that the whole scheme may be represented as follows:—

	Tall × Dwarf			Parents crossed
	Tall			F. 1, or 1st filial generation (selfed)
Tall	Tall	Tall	Dwarf	F. 2, or 2nd filial generation (selfed)
Tall (pure)	Tall and dwarf (impure)	Tall and dwarf (impure)	Dwarf (pure)	F. 3, or 3rd filial generation (selfed)

Dominant and Recessive Characters.—To the characters

of the two parents which were observed to be entire, or almost unchanged, in the hybrids, Mendel applied the term "dominant," and to those which became latent in the process, the term "recessive." The expression "recessive" was chosen because the characters in question withdraw, or entirely disappear externally, in the hybrids, but nevertheless reappear unchanged in some of their progeny. In the case of the two characters under immediate discussion the tall character is dominant to the dwarf, the latter being recessive in the first generation but reapparent (in accordance with a definite law) in their progeny. Now, if the seeds from the tall plants described as "pure" above and also those from the "pure" dwarf plant are sown the next and for any number of succeeding years, and provided selfing is continuous, the tall and dwarf plants will never produce anything but tall plants and dwarf plants respectively. The former are therefore termed "pure dominant" to distinguish them from the other or impure dominant plants, which split up into talls *and* dwarfs, but all the recessive plants remain pure indefinitely.

Two or more Pairs of Characters.—We have presented the case of one pair of contrasting characters, but no plant consists of one pair only. Mendel, as already stated, studied seven pairs in the pea, and to illustrate further the operation of his experiments we will follow the case of the two pairs of contrasting or differentiating characters—namely, (1) tall and dwarf stems, and (2) round and angular seeds. When peas bearing round seeds are crossed with others bearing wrinkled seeds the first generation (F. 1) gives round seeds: roundness is therefore dominant to wrinkledness. In this case

we may expect, if the law of unit characters is obeyed, to get

(1) Tall-stemmed plants with Round seeds
(2) " " " Wrinkled seeds
(3) Dwarf-stemmed " " Round seeds
(4) " " " Wrinkled seeds

To show all possible combinations of two pairs of contrasting characters we find that we require *sixteen* individuals. Retaining the previously ascertained proportion of tall and dwarf stems—namely, 3:1—in *sixteen* plants, there will be *twelve* with tall stems and *four* with dwarf stems—*i.e.* three to one. Round and wrinkled seeds occur in the same proportion, and consequently the twelve tall stems will produce *nine* plants with round seeds and *three* plants with wrinkled seeds. Similarly, the four plants with dwarf stems will yield *three* with round and *one* with wrinkled seeds. Again, when dealing with a single pair of contrasting characters, two pure and two impure plants were obtained in the second generation; so that, when dealing with two pairs of similar characters, there must be sixteen (4 × 4) different combinations arranged thus:

Tall-stemmed plants with Round seeds	9
" " " Wrinkled seeds	3
Dwarf-stemmed " " Round seeds	3
" plant " Wrinkled seeds	1

It follows, therefore, that if Mendel's law is true we should find, by actual trial, in the second selfed generation from the cross tall wrinkled and dwarf round, that these proportions hold good. As a fact this is what Mendel, and everyone who has tried it subsequently, has found, and not only with peas but also in the case of countless other plants and characters.

It is thus made perfectly clear by actual trial that the unit characters can be inherited independently of each other, and that the figures obtained prove the "law." The illustrations might be extended to demonstrate the result of including three or more pairs of characters, but the manner of inheritance is identical, regardless of the number involved.

The fundamental fact resulting from Mendel's experiments, then, is that in the process of reproduction the organism, whether plant or animal, does not operate as an undivisible unit, but many characters constituting that organism are inherited in definite and predicable proportions, apart from its association with other characters. The round seed in the pea, for instance, is found in plants having tall stems as well as in those having dwarf stems; similarly, wrinkled seed is present in plants with both descriptions of stems. The conception of *blending* of characters is thus replaced by that of a *recombination* of the separate characters of both parents. Further, the various units of each pair of contrasting characters can generally be distinguished when present as pure dominants, or as pure recessives, from which condition of purity they never deviate, so long, of course, as no strange pollen reaches them.

Among the dwarf stem plants there are some with round seed and others with wrinkled seed; both being recessive characters may be obtained in a state of combined purity at once, but the round peas may be members of one of two groups: either pure or impure round. Thus it is with all the different characters of the two original parents. Mendel's law enables us by growth tests to discriminate between pure or impure forms in the hybrids, so that if we desire to fix naturally dominant characters the selection

must be practised until splitting ceases—that is, until we finally hit upon forms which are pure dominants. On the other hand, if we desire to fix a recessive character, further selection is not necessary; it can appear in a pure form only.

We have seen that in the case of the pea Mendel found complete dominance of certain characters, but later investigators have shown that complete dominance is not an invariable rule: it may be partial, or the hybrid (F. 1) may exhibit characters differing from both parents. Cases such as the last-named afford a remarkably clear corroboration of Mendel's conception of the equality in the number of male and female units in operation on reproduction. For example, the Andalusian fowl, in general a blue colour, does not breed true to colour, for the offspring consists of black birds, blue birds and speckled white birds—in the proportion of one black, two blue and one white bird. When the black birds are mated together the progeny is *all* black; similarly when the whites are mated the progeny is *all* white. Black and white mated together always produce all *blues* or Andalusians again. Dominance, it should be realized, is not a necessary feature of Mendel's law of unit characters.

In the light of recent work it still remains to be ascertained whether all characters of plant and animals are inherited in accordance with the Mendelian law. The first aim of plant and animal breeders is consequently to determine which characters of the material they are dealing with behave in this way, for when once this stage is reached, the procedure of producing improved varieties of plants and breeds of animals becomes an orderly process, and it should be noted that it cannot be assumed

that what appears to be a single external character is a single Mendelian factor. Such a characteristic may be due either to one factor, or to a number of unit characters of the same kind, or to a number of dissimilar factors which in inheritance go separate ways in accordance with Mendel's law. A characteristic may even prove not to be regulated by a Mendelian factor or character at all. The matter can be settled by actual experiment and in no other manner.

Multiple Characters.—An example of the first of these cases may be given exemplifying how multiple factors or characters of the same kind may produce an intensification of what, at first sight, appears to be a single character.

Archer and Goldthorpe barleys differ in periods of growth—that is, in the length of time occupied from sowing until fully ripe—by from five to seven days, Goldthorpe being invariably the earlier of the two. Among the progeny of a cross made between the two barleys was a narrow-eared form, conspicuous by the early emergence of the ear from the leaf-sheath, and subsequently by its early ripening, for it was found to be *ten days earlier than Goldthorpe*, the earlier parent.

Again, in the progeny of a cross between Goldthorpe and Spratt—both broad-eared barleys—two forms were obtained which differed widely from the parents, one having grains placed much closer on the ear-stalk than is found in Spratt, the denser of the two parents, and the other with grains placed so far apart as to justify the classification of the barley as a narrow-eared variety. The straw of the broad-eared form, in addition, was much shorter than that of either parent.

An equally striking illustration is furnished by the work of Nilsson-Ehle, who, on crossing two red-grained wheats,

obtained varieties, some with much *redder* grain than either parent, others which were less red, and some white-grained. In all these cases it is evident that a number of factors or determinants of the same kind are present, and that when such factors meet on hybridization they may act in unison and thus produce a *cumulative* effect, resulting in the intensification of the external characteristic concerned.

These facts indicate the possibility of recombining the different characters of two or more plants, and in the possible cumulative effect of certain characters a wider potential field of improvement is opened, offering the likelihood of the ultimate production of new varieties of greater value then even the best now in use. It will be realized at the same time that nothing but actual breeding experiments can demonstrate to us the presence of these cumulative factors.

In this and the preceding chapter enough has been said to explain how the laws of heredity when ascertained and defined can be put to practical use in the production of improved plants. Precise knowledge has been acquired regarding the behaviour of the offspring of hybridized plants, and it is now possible, in many cases, to proceed by definite and predicable steps to the building up—the making of a plant of any desired combination of characters.

It will now be useful to treat a number of economic plants in detail and illustrate the advances that have been made by the scientific breeders of this century.

CHAPTER IV

RESULTS OF SCIENTIFIC PLANT BREEDING

One of the main objects of all schemes of agricultural development should be to bring to the notice of farmers the scientific work that is being carried on in all branches of their industry, to enable them to benefit to the fullest extent from such results as are obtained. In this chapter it is proposed to describe some of the most striking achievements with the principal crops, more especially those that are of particular interest to British agriculturists. As we have said, these achievements have been made possible by the application of the laws which we have endeavoured to explain and illustrate in the preceding chapters.

Wheat.—Varieties of British wheat differ from many of the imported wheats in several well-marked characteristics. The grain of home-grown wheats when cut across has a mealy appearance, sometimes more or less flecked with dull, steely patches. American and Canadian varieties usually exhibit a hard, dull, steely fracture. British varieties rarely reach the miller in as good condition as foreign sorts; they contain more moisture and are more difficult to mill "clean"—that is, to separate the flour from the bran. There are, however, more deep-seated differences, for, on baking, the flour produced from steely grain produces a larger and lighter loaf than that from mealy grain. In commerce the two kinds of grain or flour are differentiated by the terms "strong" and "weak." It is evident that a miller will prefer a "strong" wheat, for this yields him a higher percentage of flour from a given bulk of grain;

moreover, from equal weights of "strong" and "weak" flour the baker will be able to obtain a larger number of loaves from the former.

It may be possible, of course, that the "strength" found in certain foreign wheats is due to the peculiar climatic conditions under which they are grown; to test this many foreign sorts have been grown in England for a series of years. Under these conditions certain varieties show a reduction in strength, but an exception is Red Fife, a variety grown extensively in Canada and largely the basis of the wheat known as "Manitoba Hard." This variety has maintained its high milling and baking properties when grown in the British Isles. In point of yield, however, Red Fife is not equal to English varieties. The question thus at issue is whether it is possible by crossing a variety of high-yield and low-milling quality with one of low-yield and high-milling quality to produce new forms exhibiting high yield and high quality.

The efforts of Professor Sir R. H. Biffen to find a solution of this problem are widely known and appreciated. As material for investigation, Biffen chose Red Fife and Rough Chaff—the latter a typical high-yielding "weak" English variety. The first hybrid plant of these varieties yielded produce of undoubted strength, equalling, so far as could be judged, the strong parent. Amongst the progeny obtained on selfing these hybrid grains there were some plants of the second, or F. 2, generation with "strong" grain—*i.e.* grain with the Red Fife characteristics—and others with "weak" grain—*i.e.* grain with the Rough Chaff characters—the former being to the latter in the numerical proportion 3:1. Here then was segregation of two unit characters with dominance of "strong" to

"weak" grain, or grain of high-milling quality to that of low-milling quality.

Another result of very considerable economic importance proceeded from an investigation carried out on the inheritance of the resistance of different varieties of wheat to the fungoid disease known as "Yellow Rust" (*Puccinia glumarum*). English Rivet wheat was used as one parent, on account of its peculiarly well-marked resistance to the disease, and Michigan Bronze, which "is probably the most susceptible wheat to Yellow Rust in existence," as the other parent. The plants raised from the hybrid grain were at first strong and vigorous, but by the middle of the year in which they were grown the whole of their leaf surface was covered with Rust. The attack was so severe that the few small, imperfectly developed grains finally obtained failed to germinate. A further series of crosses were made between Rivet and Red King, the latter a descendant of Michigan Bronze, and, like that wheat, very susceptible to Yellow Rust. The hybrid plants were again badly rusted, but they yielded sufficient grain to raise 260 plants in the following year. Of these 195 were diseased and 64 disease-free, or a numerical ratio of three diseased plants to one disease-free plant. Thus susceptibility and resistance to ordinary Yellow Rust may be recognized as Mendelian characters, the former being dominant—a conclusion established in the second or F.2 generation, but in evidence in the first generation, for all the plants then exhibited disease to an unmistakable extent.

These results formed a most important basis for plant improvement. The first outcome of their application was Little Joss, a variety obtained by Biffen by crossing Square

Head Master and Ghirka. Succeeding this, Yeoman I, a high-quality wheat, produced by crossing Red Fife and Browicks, was introduced, and has proved a valuable addition to the list of British wheats. Recently Yeoman II, a selection from Yeoman I, but of higher baking value, has been placed on the market.

As illustrating the value of another plant character —namely, earliness in ripening—reference may be appropriately made here to Marquis wheat, which has been rightly described as the greatest success of the scientific plant breeder. In 1918, 20,000,000 acres in Canada and the United States of America were sown with Marquis, whilst the produce in that year was estimated at over 300,000,000 bushels. Before 1909 the principal variety grown in Canada was Red Fife—a variety with the peculiar qualities already mentioned. The period of growth of wheat in Canada ranges from about one hundred to one hundred and forty days, varying with the season and the locality; but in the Northern districts, even with this short period, the ripening grain is in constant danger of injury from early autumn frosts. Once the ripening grain is frosted it fails to fill properly, and is then totally unsuitable for milling.

An early-ripening wheat is thus a necessity, for this character alone often means the difference between complete success and equally complete failure. With this object in view, Dr William Saunders, the organizer and first Director of the Dominion Experimental Farms, obtained samples of wheat from all the great wheat-growing countries and from different altitudes in the Himalaya Mountains of India and tested them under Canadian conditions. Later, he made a number of crosses between Red Fife and varieties

exhibiting earliness in ripening, the particular character he sought. One of these crosses was *Red Fife* and *Hard Red Calcutta*, the latter an early-ripening Indian wheat. From the progeny of this cross Dr Charles E. Saunders in 1903 selected a single promising plant and propagated it separately for several seasons. Tests of milling quality were made yearly on the limited quantity of material available, and these indicated high quality. In 1909 Marquis, as the new wheat was now named, was distributed to wheat-growers generally, with the results that have been indicated.

Barley.—In 1901 the Irish Department of Agriculture, in collaboration with Messrs Arthur Guinness & Company, Dublin, began a series of experiments designed to improve the Irish barley crop. A series of field trials conducted for a number of years furnished conclusive evidence that barleys of the Archer type were the most remunerative to the grower in all of the barley-growing districts, and, fortunately, this barley was ascertained to be superior also for malting and brewing. The commercial Archer barley used in the field trials was, however, impure, for it consisted of a number of different strains of Archer, differing in obvious characters, such as strength of straw and time of ripening, and probably in yield of grain and malting quality.

Good malting barley is characterized by a low protein content and is, therefore, in this respect just the opposite to good milling wheat. Another essential of a good malting sample is evenness in size and composition of the grain—a condition manifestly unattainable unless all the plants composing the crop ripen at the same time. It is known that certain varieties, quite irrespective of the conditions under which they are grown, are invariably poor malting

material; but apart from what may be termed the individuality of a variety—that is, its ability to produce grain with high or low malting quality—it is never possible to get high quality unless the grain is fully ripened. In the same way the best yield is unattainable unless the plant is allowed time to complete the transference of material from the straw to the grain. Consequently we arrive at the conclusion that neither maximum yield nor quality is possible unless all the plants composing a crop are equally and fully ripened.

A number of single plants were selected from crops of commercial Archer and grown separately under controlled conditions. Ultimately after careful comparison one was chosen for further propagation, which, when eventually tested with the parent stock from which it was taken, was found to be superior in yield of grain by 3 bushels (12 stones) per acre. The grain in addition exhibited greater evenness in size and higher malting quality.

This selection, named Archer I, exhibited the defect common to all Archers in Ireland—it was late in ripening in the average season. A search was made for an earlier type, and a selection, Archer II, was eventually obtained which was slightly superior to Archer I in yield and from three to five days earlier in ripening. Neither Archer I nor Archer II, however, possessed as strong a straw as is desirable under the conditions prevailing in Ireland, and after further, but unsuccessful, attempts to secure a type with this characteristic, the production of a new variety by crossing was attempted. For this purpose Archer I and Spratt were used as parents. From the various broad- and narrow-eared forms produced in the second generation of

the hybrid, a narrow-eared plant showing good, stiff straw, abundant tillering, and grain of good size and quality was selected. Further selections, based on comparative yield tests, were made on the progeny of this plant, and one of them, named Spratt-Archer, was eventually increased until sufficient seed was available to test it with the parent Archer I in field plots. The new barley then proved superior to Archer I in standing power, and was in addition about three days earlier in ripening. It also produced a higher yield of grain which was at the same time better malting material. Thus, on the average of five years' tests, Spratt-Archer produced 4¼ bushels (17 stones) of grain per acre more than Archer I.

So marked is the value of this barley to the farmer, maltster and brewer that, although introduced into general cultivation in Ireland only in 1919, fully 90 per cent. of the barley area in that country is now sown with it. It is also grown extensively in Norfolk and neighbouring counties in the east of England, and has established itself in other counties as widely apart as Devon and York.

Of English broad-eared barleys, Goldthorpe is one of the best in point of yield, and one of the best, if not the best, in point of malting quality. Unfortunately the straw of this variety is long and becomes brittle on ripening, with the result that the ears are liable to break off the straw, especially in dry seasons or during heavy winds. If the straw, or more particularly the "neck," which is the length of the straw from the point at which the uppermost leaf-blade is given off to the base of the ear, could be shortened, it appeared as if the loss would be considerably reduced. With this object in view, Dr E. S. Beaven of Warminster crossed Plumage, a broad-eared variety closely

resembling Goldthorpe, with Archer, the latter being characterized by short, erect straw and relatively short "neck." From amongst the plants of the second generation Beaven selected a broad-eared, short-necked form, which he named Plumage-Archer. This barley proved superior to Goldthorpe in the sense that the loss from brittleness was now obviated. It has further been shown to yield well, to possess high malting quality, and to be sufficiently early in ripening to permit of it being grown successfully as far north as the Lowlands of Scotland.

A variety of similar character was obtained during the course of the Irish experiments by crossing Archer I and Goldthorpe. Here again the straw and neck of the form finally selected were short and erect and the malting quality high. This variety—Archer-Goldthorpe—is distinctly early in ripening, and can be grown successfully on heavier soils and in later-ripening districts with greater chances of success than either parent.

Oats.—As the oat crop is valued for both its grain and its straw, it presents an additional problem in improvement to those found in wheat and barley, for not only the standing power but the suitability of the straw for feeding must be considered. Clearly defined differences in this respect provide ample material for the exercise of selection.

In the Midland and Southern districts of the British Isles, however, successful cultivation of the oat depends largely on evading the ravages of frit-fly. One safeguard against this pest is the early and strong development of the plant, to obtain which it is necessary to sow early. A still more powerful defence is found in autumn sowing, but this involves the use of winter-hardy varieties, of which the majority are grey- or black-grained. In some places there

is a prejudice in favour of white oats, and to supply this demand, and at the same time to improve, if possible, the yield and character of the grain, cross-fertilizing experiments have been conducted, and are still in progress at the Plant Breeding Institute, Cambridge. Varieties such as Grey and Black Winter, which are known to be winter-hardy, have been crossed with good spring oats like Victory and Thousand Dollar, and from the produce it has been possible to select forms possessing some of the attributes, such as the prostrate habit of growth, of winter varieties.

The Ministry of Agriculture, Belfast, is also conducting breeding experiments with the oat crop, which is extremely important in Northern Ireland. The guiding object in this case is the raising of varieties with high-milling values and the provision thereby of good quality grain for the oatmeal-milling industry, associated with straw of high value for cattle feeding.

Flax.—The economic value of the flax crop—the raw material of linen manufacture—is measured by the quantity and quality of fibre obtained from the plant after scutching—a mechanical operation resulting in the separation of the pith of the plant from the fibrous and more valuable portion. The fibres are present towards the outside and run the whole length of the plant. The value of a sample of scutched flax is determined largely by the length and fineness of the fibres, as the description and quality of the manufactured linen depend on these characteristics of the raw material. The ideal plant for linen production is one devoid of branches, long and fine—that is, with a thin stem. If the flax grower produces as thick a crop as possible, always having regard to its ability to

remain standing until sufficiently ripe for pulling, he may to that extent control the fineness of the resulting flax, but he cannot thereby materially alter the length of the fibre.

The Irish Department of Agriculture began a series of selection experiments in 1911. Flax is normally self-fertilizing and is not therefore subject to differences in length resulting from crossing with other plants. The procedure adopted, therefore, was to pick out from an unselected crop or population a number of plants showing decided superiority in length and fineness. These were grown separately for two or three seasons in order to make sure that the length was a true expression of their character and not due to chance external conditions, such as differences in the quality of the soil or manuring. Subsequently the two most promising lines, Nos. 3 and 5, were propagated separately until 1919, when sufficient seed was available to compare them with the seed ordinarily in use in the country.

From the striking uniformity of the flax straw then produced from each of the pure lines compared with that grown from any of the commercial varieties, and from the results of the comparative field trials, it is clearly evident that the flax crop, like wheat, barley and oats, can be greatly improved by the propagation of seed from single selected plants.

Turnips and Mangolds.—The Danish work with root crops furnishes an interesting and instructive example of what may be accomplished in this direction.

The stimulus to improvement of these crops was provided by a very complete series of stock-feeding experiments conducted by H. J. Fford of the Royal Agricultural

College, Copenhagen, commencing about 1883. Fford set out to determine the comparative feeding values of various commonly used materials, but more especially the proper economic value of the root crops when used in conjunction with the rations usually employed in Denmark. These, with other of Fford's results, were responsible for an extraordinary increase in the acreage under roots, mangolds, swedes and turnips in Denmark, as will be seen from the following figures:—

1888 . . .	95,000 acres
1896 . . .	180,000 ,,
1901 . . .	330,000 ,,
1907 . . .	565,000 ,,
1912 . . .	627,000 ,,
1919 . . .	678,000 ,,

At about the same time that Fford was engaged on his feeding-value investigations a series of variety tests with root crops was started by the "Society for Improving Cultivated Plants," the object being to find out which varieties, and which individual strain within the variety, gave the highest yield of solids per acre. Subsequently a State Committee on Plant Culture was formed, and Helweg, who was in charge of the root tests at that time, was appointed the Danish Government's Root Commissioner, which post he retained until his death in 1920.

Throughout the whole period of the work the yield of solids in the roots from every experimental centre was determined, and the value of every variety and of every strain of that variety submitted for examination was decided on the basis of yield of *dry matter per acre.* With the

assistance of the annual reports on these experiments, and as a result of Helweg's personal influence with the various Danish root seed-growers, inferior strains and varieties of roots were gradually eliminated and their place taken by those that had been proved superior in yield of dry matter per acre.

Sugar-beet. — Sugar-beet is a crop of considerable economic importance on the Continent, where it has been grown on an ever-increasing scale during the past one hundred years. The first sugar factory was founded at Cunern in Silesia in 1802, and shortly afterwards Mathieu de Dombasle established a similar factory in France. In 1786 Achard organized field experiments with sugar-beet at Clansdorf, near Berlin, and his name is associated with a variety known as the *White Sugar-beet of Silesia*, which was introduced into France in 1775 by Philippe-Victoire de Vilmorin, a member of the celebrated French seed firm to whose efforts for many years past the commercial improvement of this crop is largely due. The whole of the improvement obtained by Messrs Vilmorin centres round the *White Silesian Sugar-beet.*

In this plant there were two clearly defined lines for improvement: one was the enrichment of the sugar content of the root, the other the increase in the weight of the root, the two together operating in the direction of a greater total quantity of sugar per acre. A further property of the root demanded attention even in the early experimental stage, and is insistent to-day, and that is the facility with which it can be pulled from the ground. To all these aspects Louis de Vilmorin (1816-1860) applied a rigorous selection, and was thereby enabled to introduce forms with shorter and more shouldered root and

thus easier to pull, possessing at the same time a higher percentage of sugar and yielding a heavier crop per acre.

It should, however, be realized that, so far, no scientifically pure lines of sugar-beet have been isolated. For many years, particularly in the large seed establishments in Germany, the method practised has been essentially mass selection, of which the result has been to isolate a population of a high average sugar content.

Sugar-beet is a cross-fertilizing plant; the pollen is light and abundant and is carried long distances by the wind. This fact accounts for many of the variations observed in the progeny of these mass-selected beets. In the early days, when the investigations were directed by Louis de Vilmorin, mother roots—that is, roots that were intended to be seed-bearers—were selected on the basis of their general form, freedom from side roots, single neck, weight and sugar content. The mother roots were allowed to seed and the produce raised therefrom was again subject to a similar selection. Amongst the roots selected on points of form there was always a large variation in sugar content, some being high, others quite markedly low, and a considerable number of intermediate value. Of the mother roots finally chosen as seed-bearers, some maintained a high sugar content in their progeny, but many showed a mean value. Having regard to the free natural cross-fertilizing, this is not to be wondered at, for it is evident that the original White Silesian Beet was in reality a hybrid and that sugar content may be regarded as a transmittible character.

These considerations led Messrs Vilmorin to elaborate their methods of selection of mother roots still further, and

to self the selected roots under silk covers, through which it is impossible for foreign pollen to pass. The number of seeds obtained under these conditions is very much reduced and the plants grown from such seeds suffer in vigour, but to be set against these drawbacks is the possibility of determining by means of the progeny the exact constitution of the parent in point of sugar content. Finally, after further treatment in this way, the two parents exhibiting high sugar content with the smallest variation and otherwise similar in character are crossed together, thus restoring the vigour temporarily lost by self-fertilization, but maintaining freedom from wide variations in the progeny.

The various steps in improvement may be shown as follows: from 1838 to 1869 the mean content of sugar rose from 8·8 per cent. to 10·1 per cent.; from 1868 to 1888 it rose to 13·7 per cent., and from 1888 to 1912 to 18·5 per cent. From 1912 to 1922 various lines have been obtained with a slightly higher sugar content.

Wild beets have been found with 20 per cent. of sugar, and amongst cultivated beets cases of 21 per cent. have been recorded. In practice the difficulty is and will always be to secure the progeny of plants of this character free from the influence of pollen of inferior lots. Provided measures are taken to secure immunity from cross-pollination, however, further progress appears to be possible by the continual propagation of superior lines. There must necessarily be limits to the extent to which sugar content alone can be secured without possibly affecting the constitution of the plant, but there is no evidence that such a stage has been reached yet.

We have dealt at some length with the recent improvements in wheat, barley, oats, roots and sugar-beet.

Consideration of space precludes more than a hasty survey of the remaining farm crops, in relation to many of which, although active work is in progress, no considerable practical results are yet to hand; or, to speak more correctly, the professedly scientific improvements have not yet been placed on the market.

Forage Plants.—The improvement of forage plants such as the ordinary agricultural grasses has been the subject of investigation at Svalöf (Sweden), in Denmark, and in the United States of America; recently work of this description has been undertaken in this country by Professor Stapledon at the Welsh Plant Breeding Station, Aberystwyth. As a result of these studies it has been shown that the grasses ordinarily in use consist, as in the closely allied cereals, of large numbers of forms differing in such characters as height, tillering capacity, size of leaf, erect or semi-erect habit of growth, colour of the leaf, and ability of the plant to remain green until ready for cutting, etc.

The value of forage plants to the grower depends on the quantity of stalk and leaf produced; he is not generally interested in seed production. The many differing forms present in the produce of unselected seed permit of selection being made on this basis, and several improved lines of timothy and rye grass have been placed on the market already.

It should be noted that the plants capable of producing the largest quantities of stalk and leaf are usually relatively poor seed-yielders—a fact that may present some difficulty to the seed-grower and has consequently tended to the marketing of seed-producing types. As, however, the value of the crop is the amount of forage it produces, the

seed of selections exhibiting superiority in this respect will always command a higher price on the market than unselected seed.

Although closely allied to the cereals botanically, grasses differ from them in the facility with which they cross-pollinate — a circumstance involving difficulty in obtaining stocks of pure seed. Fortunately for scientific workers most grasses are readily propagated vegetatively by detaching the various tillers from the mother plant and propagating them separately. In this way the characters of a selection may be studied for as long a period as is desired. Further, when it is necessary to return to seed-production again, the larger number of plants available for the purpose by their very numbers render the procedure of exclusion of foreign pollen much easier.

Clovers.—A critical study of clovers demonstrates a wide range of forms in all the varieties commonly sown. Amongst red clover, for instance, plants are found differing in the time of flowering, the length of the flower stalk, erectness or proneness of habit of growth, and in the profusion of foliage. It is quite possible that they differ in their permanency—a character of sufficient economic importance to justify extended investigation. Amongst white clovers the isolation of the most permanent forms is a line of inquiry of pressing necessity to-day.

Somewhat serious difficulties meet the clover breeder at the very outset, for the crop is largely self-sterile—*i.e.* it requires foreign pollen to secure fertilization of the seed. The best means of obtaining this, with the minimum risk of cross-pollination by inferior sorts, is still a subject for investigation. In some experiments made at Aberystwyth the inter-pollination of similar forms has been effected by

growing two plants under muslin and introducing humble bees. These insects seem to be specially adapted by nature to effect the fertilization of the clover flower. The prominent fact which emerges from the Aberystwyth investigations is the superiority for forage purposes of the indigenous clovers of the British Isles to clovers grown abroad—in Italy, Chile, etc.—most of which owe their predominance in the markets to their seed-producing rather than their herbage-producing qualities.

Potatoes.—The economic importance of the potato crop and its susceptibility to a number of formidable diseases have compelled the attention of plant breeders and plant pathologists in many countries. The origin and history of the potato are outside the range of this book: it will suffice to say that the plant as we know it to-day originated in material imported from South America about the end of the sixteenth century. Whether the material contained tubers derived from more than one species is debatable. The important historical fact is that under cultivation the size, regularity of shape and flavour of the tuber have been improved, with the result that to-day large, well-shaped and smooth-skinned tubers of good flavour are the successors of the small, rough, irregularly sized, strongly flavoured tubers of earlier times.

The potato differs from most agricultural crops in that it is not usually reproduced from a true seed, but from a tuber, which is an elaborated portion of the underground stem. Thus the changes noted in the tubers are the result of hybridization and of selection of variations occurring in that part of the plant. These improvements, economically useful as they are, are of minor importance compared with the resistance of the plant to various diseases. For many

years potato-blight (*Phytophthora infestans*) was a source of serious trouble. In seasons when the disease became epidemic the crop was almost completely destroyed, as for instance in Ireland in 1846. To a large extent the severity of subsequent attacks was reduced by breeding varieties, such as Champion, which possessed a certain degree of resistance. In more modern times the practice of spraying the crop with sulphate of copper in various forms has reduced the risks of attack very materially.

Recently the occurrence and spread of the potato Wart Disease have presented a serious problem. Fortunately this has been met by the discovery that some varieties are immune to wart disease; but while they approach many of the susceptible varieties in yield they are not, as a whole, equal to the latter for commercial and culinary purposes. These circumstances raise the question of the production of new varieties possessing immunity combined with good edible qualities. As a result of cross-fertilizing the potato flower, and thus returning to a true-seed generation, Dr Salaman and his collaborators have succeeded in showing that immunity and susceptibility to wart disease are probably Mendelian factors and segregate in the hybrid seedlings. With an extension of these studies to the more subtle characters which go to make up yield and quality there is legitimate reason to hope that new forms possessing combinations of desirable characters will eventually be produced. That the process will be long is evident from the fact that all of our potato varieties are hybrids: this may be readily determined by growing the seed from a selfed "apple" of any variety, when the resulting seedlings display a wide range in the haulm, and in the shape, size and colour of the tubers. It is therefore fortunate that when repro-

duced from the tuber the plant shows very little, if any, variation.

Leaf-curl, mosaic and allied diseases, known collectively as virus diseases, are still engaging the attention of plant pathologists. Their relation to one another is debatable, but there is unanimity of opinion that their presence is detrimental to the yield of the crop. It has been shown that leaf-curl, etc., may be communicated from diseased to healthy plants by means of aphides (green-flies), but no means of controlling infection is available other than that of excluding insects by means of suitable covers—an impracticable defence on a large scale.

Green-flies and insects generally are less numerous in the northern and north-western districts of the British Isles, and here it is observed that the incidence of the disease is very much less severe, and clean "seed" is consequently much easier to obtain. This, no doubt, is the reason for the practice of bringing seed potatoes from northern to southern districts. It is noteworthy that once a stock of seed is diseased, however slightly, it will not recover by being grown in disease-free districts.

It may be possible to raise varieties immune to leaf-curl; a few are already known, and this leads one to hope that others will be obtained. The experimental evidence of recent years does not support the claim of degeneration in the potato if by that is meant a change resulting from senility. Many of the oldest varietios may still be seen growing in various localities where they have been under cultivation, often in the same garden and without change of seed, for long periods. When removed from these to other districts there is, frequently, a progressive loss in all the attributes of the plant, until it is finally destroyed

entirely, and this can be readily traced to the leaf-curl disease.

Increased Vigour due to Crossing.—In conclusion, reference may be made to the increased vigour obtained on crossing varieties of plants and certain breeds of animals—a phenomenon to which the term *heterosis* has been applied. The occurrence of increased vigour in hybrids has claimed attention for many years. Darwin gives a detailed account of his experiments and results obtained with hybrid plants in his *Cross and Self Fertilisation of Plants*; it was also noted by Mendel in the course of his studies with peas, for he states that, in repeated experiments, stems of 1 foot and 6 feet in length yielded, without exception, hybrids which varied in length between 6 feet and 7½ feet.

The subject has reached prominence in more recent years in the course of various maize-breeding experiments conducted in America. Maize is self-fertile, but is generally cross-fertilized in the field. On selfing this plant—*i.e.* fertilizing it with its own pollen for a series of generations—the resulting plants exhibit a gradual reduction of vigour and productivity until a stage is finally reached after which no further reduction occurs, however long the "selfing" is continued. This point, in the opinion of some investigators, represents a return to a condition of germinal purity, or, in other words, a pure-line condition is reached. Now if two separate varieties, both of which have been selfed until this state of purity is reached, are crossed, the resulting plants become immediately most luxuriant and productive. Practical use is made of this result by sowing seeds of the inbred or pure varieties it is desired to cross in alternate rows and detasselling—that is, removing the anthers of one

variety. The seeds then obtained in the detasselled plants will be hybrids, for they can be fertilized only by foreign pollen, and that from immediately adjoining rows is the nearest and most likely to effect this. If the vigorous plants obtained in this way are selfed, they show a decrease in vigour. The greatest decrease is apparent in the first generation of selfed seeds, but it continues until a condition resembling that of the original parents is reached. Thus we cannot regard hybrid vigour as exhibiting a strictly Mendelian inheritance in the sense that the effect is always traceable to unit characters affecting vigour. If it did, we should secure some forms with vigour equal to that of the first generation in every succeeding generation, but, so far, the occurrence of such individuals has not been observed.

It will be recollected that evidence of an effect of this nature is furnished by Vilmorin's sugar-beet. In this case, after selfing selected mother roots there was a very noticeable reduction in the vigour of the resulting plants and in the number of seeds they set; but when plants raised from seeds obtained in this way were crossed, there was an immediate return of vegetative vigour, accompanied by a large increase in seed-production.

A further example is supplied by the work of Henry, who on crossing certain varieties of forest trees obtained hybrids characterized by vigour and a rapidity of growth greatly in advance of either parent. A hybrid poplar (*Populus generosa*), for instance, was obtained in 1912 by crossing two distinct species. By the end of October of that year the hybrid seedlings were 2 inches high; by the end of 1913 four seedlings measured 3 feet 6 inches, 3 feet 1 inch, 3 feet, and 2 feet 11 inches, respectively. At

the end of 1914 two of these four seedlings measured 7 feet 6 inches and 10 feet 1 inch respectively.

It is clear from what has already been said that it is impossible to take practical advantage of heterosis in our cereals, because these are closely self-fertilizing. It is, however, a question worth investigating whether some advantage would not result with grasses, for here there is always a certain amount of outcrossing, and vegetative development is the main consideration.

Similarly with forage plants such as cabbage, kale and kohl-rabi, which are usually self-fertile but commonly cross-pollinated, it may be possible to secure an advantage sufficiently remunerative to compensate for the outlay involved in selfing desirable selections for a series of generations.

The ultimate causes of heterosis are still matters of speculation, but one interesting fact has been established. When two plants arising from the same pure line are selfed for a number of generations and then crossed, heterosis does not occur. This points to the diversity of the germinal constitution in the two parents as being in some manner the fundamental operating cause.

Plant Characters subsidiary to Yield.—It will be observed that many of the plant characters used as illustrations of crop improvement are subsidiary to yield. Resistance to disease attains its maximum economic value only when it is found in conjunction with a potentially high-yielding variety; earliness in ripening and modifications of the character of straw, eliminating serious losses of the ripened grain, may be regarded in a similar light. Improvements in the quality of the crop may be of such a character and degree as to increase its economic value apart from

yield, but there are indications, as in sugar-beet for instance that a limit to progress in this direction may be reached beyond which further advance is accompanied by a tendency to decrease the vitality of the plant, unless, indeed entirely novel forms can be produced.

Although there is no reason to anticipate such a condition arising in cereals, it is nevertheless clear that, having once obtained a good standard of quality, it is to increases in the yield of grain we must look for enhancement of the economic value of crops. Certain considerations on the subject of breeding for yield in cereals may therefore be presented.

Breeding for Yield in Cereals.—To those who are in the habit of observing cereal crops in all stages of growth it is well known that varieties differ in their ability to produce tillers capable of contributing to the yield of grain of the plant. They also differ in the number of grains per ear, in the size and weight of each grain, and in earliness and lateness in ripening. There is general agreement that the extent to which a plant tillers is a measure of the fertility of the soil in which it grows—the more fertile the soil the greater the number of tillers produced. This is particularly evident when plants are widely spaced and can then draw on a correspondingly large area for their food supplies. Such is a general statement of observed facts; but what primarily constitutes the cause of one variety tillering more than another is a question for which we still await an answer. It seems, at first sight, that if one variety produces more grain-bearing tillers than another its greater grain-producing capacity is thereby established beyond question. Such an assumption, however, is evidently made regardless of the fact that the number and size of the

grains in different ears differ in a varietal sense also, and the relation between the number of tillers and number and weight of grains must also be taken into account.

A further very important characteristic of a variety—the earliness or lateness in ripening—must also be included in any general description of the factors of yield, and this again must be viewed in relation to the general climatic conditions under which the crop is grown. Some idea of the importance of this factor will be realized from the example of Marquis wheat already quoted, page 42. In the British Isles the importance of earliness is by no means negligible, and some attention to this point alone would be of unquestionable value in northern and western districts, more especially those characterized by a heavy annual rainfall.

In addition to being differentiated by the number of tillers, varieties can be distinguished by the time and the rate at which these are produced. This in itself may exert an important influence on yield, for as the tillers develop and appear at different dates, and all require time to reach full development, it follows that the smaller the difference in time of appearances the larger will be their final contribution to the total yield of grain of the plant. How far the various tillers develop and finally influence the yield depends largely on the character of the season. In wet, sunless years development will be interfered with in proportion to the earliness or lateness of the variety, whereas in dry seasons a late-ripening variety, owing to its habit of slower ripening, may fill its grain more completely and at the same time avoid incomplete development resulting from premature ripening.

If it were possible to add materially to the number or

size, or both, of the grains of the cereal ear, the other plant features, such as tillering, might not be regarded of such importance, but at no time are we likely to effect improvement without a due regard to all the factors concurrently.

Finally, it should be pointed out that the yield of an individual plant may be a very different thing from yield per acre. The latter can be increased in the opposing ways, either by increasing the number of plants with comparatively few tillers, or by increasing the tillers of the existing plants: in both cases the limit is the number of possible ears per acre.

With so many factors in operation the best combination of characters is not easily defined. Sufficient has been said, however, to indicate the general lines on which the question may be approached, and although much time and individual study of our varieties of crops is involved, there is ample justification in many results already obtained to warrant hopes of further advance, however slow that may necessarily be.

SUMMARY

In this and the preceding chapter we have dealt with selection and hybridization as the two master principles of plant improvement. It has been shown that selection to be of any value should begin with the isolation and protection from foreign pollen of single plants. The selfed progeny of these single plants must first of all be examined in order to ascertain to what extent it is true to the characters exhibited by the original parent. If wide variation exists, selfing must be carried on to another generation, and if necessary succeeding generations, until plants are found

which do breed true. If it is desired to build up a stock of the type, the process must start again from a single plant.

It has been shown that if the crop operated on is invariably self-fertilizing by nature—and in regard to cereals this is the case—the process is simpler. As contamination from outside is infrequent, a stock can be rapidly built up. Here the process of selection pure and simple ends. We have produced nothing new. In the language of plant breeders we have simply "pure-lined" the crop. If we wish to go a step farther, cross-fertilization between two pure lines is effected. We know then that in the *second* selfed generation we shall find not only every possible recombination of the characters present in the parents, but also, possibly, new characteristics either in the form of the intensification of their qualities, or of true-breeding recessive characters which had been lying dormant in the parents. A process of selection begins again. We must pure-line the F. 2 generation, starting as before with single plants. We wish particularly to emphasize that these methods are deliberate—"according to plan": each step is taken with a definite object in view, and it is known beforehand what will happen and what the next step should be. As the scientific breeder found it, the art of plant improvement was haphazard. Both selection and hybridization were being practised, but no law or order prevailed. The only merit that the scientific breeder claims is that he has introduced law, knows what he should do, the reason why he does it, and what he should do next. One other feature that distinguishes scientific work deserves to be emphasized: it is all based on accurate observation, and accurate observation includes measuring, counting and weighing.

Opportunities of improvement are not confined to any particular functions of the plant. They may be found, for instance, in what are termed morphological characters—that is, characters of the form of the plant, such as those of the leaf, stem, roots, etc.; in physiological characters such as the length of period of growth; inability to resist disease; and finally in yield and quality. Crop plants differ in their response to the conditions of soil and climate under which they are grown, and it is evident that their economic suitability will be limited thereby. There is a considerable range of adaptability amongst crop plants to these conditions, but it is highly improbable that any one variety will be found suitable for all parts of the country.

CHAPTER V

MARKETING OF IMPROVED PLANTS

In this chapter it is proposed to give some consideration to the problem of marketing improved plants. Having by scientific methods, or otherwise, obtained an improved plant or pure line, what are the best means of securing its adoption by the farmer? It is one thing to breed an improved plant, it is quite another (and raises problems normally outside the domain of the scientist) to introduce it into commerce and maintain its purity on the markets. As matters stand in this country, it has been left practically entirely to the seedsman to effect the introduction of an improved crop, and it must not be forgotten that his commercial interests may differ from those of the grower. Broadly speaking, new varieties owe some part of their value for the seedsman merely to their novelty; to the grower and seller of the produce the novelty does not so much matter. What is important is that the crop of the improved plant should be more valuable than that of the varieties already on the market to a degree which will recompense the grower for the inevitably higher price he has to pay for the novelty.

In the next place, it should be pointed out that there is another important consideration in relation to the marketing of an improved plant, and that is, what are the chances of its remaining pure? If profitable to grow, will it be possible to buy seed on the market year after year of the same high standard as it possessed when it left the hands of the breeder? The answer to this question depends largely upon whether the plant in question is normally self-fertilized or not. If the plant crosses with others

readily, it is obvious that it will suffer contamination from the proximity of a crop of the variety which it is intended to replace. If, on the other hand, the flower of the new plant is self-fertile, there is no such danger, and commercial stocks of the seed will readily be obtainable in a pure condition year after year. All the commonly grown cereals—wheat, barley and oats—are of this description : so far as the plant itself is concerned contamination is impossible ; the risks that exist outside the plant will be described subsequently. An example of the other class is provided by the *Brassicæ* (turnips, cabbage, etc.) family ; these, when grown for seed, are readily fertilized by strange pollen. In their case the growing for seed must be surrounded (as it is by the best growers) with special precautions.

"**Degeneration.**"—In this connexion mention must be made of other considerations. For example, one frequently hears it asserted that stocks of seed of certain crops are "degenerating" or reverting, and, as a large proportion of the seed used annually is either grown by the farmer himself or obtained from neighbouring farmers, it is desirable to ascertain how far such a statement has a basis in actual fact. As pointed out above, cereals are normally self-fertilized, and no evidence is yet forthcoming that pure lines of these plants exhibit a progressive decrease in value in point of either yield or quality : cereals, as grown, remain, in effect, pure lines.

It is, nevertheless, quite frequently possible to observe a distinct falling-off in the size and weight of grain and in other quantitative characters of some varieties when grown on certain soils and under some climatic conditions. These, however, are only temporary and non-heritable

modifications, having no foundation in the germ of the seed; the variety will assume its more usual characteristics immediately it is grown again under conditions to which it is better suited. Potato oats may be quoted as an example: in Scotland, generally, and in Northern Ireland the grain of this variety is usually remarkably well filled, whilst in the south of England, owing to the smaller rainfall and to the warmer climate and consequently quicker ripening, the same oat is frequently thin and poorly filled. If, however, seed of Potato oat taken from a crop grown in England is grown in Scotland, it will rapidly assume the characteristics by which it is so well known there.

There are many similar examples of the adjustment of varieties to definite soil and climatic conditions, but they may all be regarded as temporary effects and, as such, incapable of causing definite and permanent changes in varieties. Potato oat may be an extreme case, but it exemplifies a condition to which full weight must be given when the distribution of new varieties is under consideration.

There is danger, when viewing the results of comparative variety trials, of ascribing ascertained differences in, say, yield, to the varieties themselves without due regard to what may be an effect on the variety produced by the soil and the climate, either singly or in combination. The various characters of plants which go to make up a resultant, which we express as "yield," are not yet clearly defined. In cereals they are probably a combination of the number of grains, size of grains, tillering capacity and an ability to ripen early, but what stimulates any one character to a greater extent in some conditions than in

others is still undetermined. Thus, in comparing varieties we are in reality only determining their relative suitability for the particular conditions under which they are grown.

Archer barley may be used as an illustration. This variety is grown extensively in the east and south and south-east of England, where, on account of its high productivity and generally good malting quality, it has been in cultivation for many years. The conditions in these districts tend to early ripening. Once Archer is removed to later-ripening districts it is apparent, however, that it is in reality relatively late ripening, and as we proceed in a northerly or westerly direction its cultivation gradually decreases until on reaching Scotland it is very rarely found at all. A test of Archer and other varieties in Scotland would give an erroneous idea of the full capabilities of the variety, for in a cold wet season the yield would be unduly low for similar, but opposite, reasons that the Potato oat is so poor in the south of England. In so far, then, as the term "degeneration" is applied to changes brought about by conditions of this nature its use is justified, but only within the prescribed limits of temporary changes, always bearing in mind that these changes are not heritable.

Unchanging Characters and Admixtures.—In an earlier chapter we showed that it is possible to select from the progeny of a hybrid pure forms capable of maintaining their characters unchanged through numberless generations. Provided sufficient care has been exercised in selecting these pure forms, and that the plant is self-fertile, there is no reason why they should not remain in this condition of purity. The invisible characters, such for instance as "quality" in any one of the cereals, are

admittedly more difficult to fix; but here again their permanency depends on the care exercised in selection. It is not claimed that there have not been cases in which changes of a very apparent nature have occurred, such for instance as the forms resembling the wild oat found in certain oats, but these changes are not incidental to hybrids generally, when properly selected.

When speaking of Archer barley in connexion with the Irish experiment (p. 44) it was shown how an increased yield of grain was obtained by growing seed from a *selected single plant*, thereby not only assuring the propagation of a superior form, but also eliminating the diversity of types found in crops grown from commercial seed. But if an increase in yield can be obtained by eliminating strange types, a reduction in yield will also be obtained by the reverse process—that is, by any accidental addition of unlike forms from outside. In selecting a single plant for extended propagation every effort is made to ensure that it is the best in every respect for the conditions under which it will be grown. Still, it is always possible, though not very probable, that some of the strangers are more prolific than the pure-line crop in which they occur, but if that be so, and provided the particular mixture is desirable in all other features, then its substitution for the pure line in hand would be the proper procedure.

More usually the strangers are inferior in yield or quality to the crop in which they are found, and their presence consequently reduces the final value of the crop. They may also be either earlier or later in ripening than the main crop: in the former case they probably sustain loss by grains becoming overripe and falling off the ear, and in the latter case their yield is reduced because they

are not completely ripened. Similarly in regard to quality: evenness in composition, which is becoming every year more necessary, is difficult to obtain when the crop consists of different types; for amongst other things varieties exhibit differences in size of grain. If to such differences the qualities in ripening are added, there will be corresponding lowering in both apparent and actual quality. Here then is the primary cause of the occasional deterioration in the productivity and quality of cereal crops. If for any reason the strangers increase more rapidly than the majority of the plants composing the crop, the changes involved will be progressively more harmful from year to year.

How Mixtures may arise.—Fortunately, mixtures in cereals do not ordinarily arise as a result of deep-seated changes in plants themselves, in which case they would be difficult to control; they are generally contaminations brought in by mechanical agencies. Where several varieties of one cereal are grown on one farm, or more especially in one field, it is extremely easy for grains of the varieties to become mixed, either during sowing, or particularly during harvesting. The most prolific source of mixed types is the thrashing machine, for there is great difficulty in removing from the machine every grain of a previously thrashed crop. Nevertheless, much may be done to minimize mixing, by adopting simple measures, such as brushing the machine down thoroughly before commencing to thrash; by opening and cleaning the hummeller box and the slide at the bottom of the grain-elevator box; by running the machine empty for a time between each variety, and, finally, by discarding for seed purposes the first two sacks of grain of each variety that come through the machine, for these probably contain the

most readily dislodged grains of previous varieties from inaccessible parts of the mill.

Another circumstance complicating the position to-day is the fact of the likeness of some improved varieties to one or another of the parents from which they were raised, and from which they may differ in varying degrees of quality or yield only. Thus Spratt-Archer, in grain characters, is practically indistinguishable from Archer, and Yeoman II from Yeoman I. In the former, however, there are certain differences visible in the young plants of the parent and the hybrid, but none apparently in the latter. Thus, if the agricultural community is to obtain the full benefit of improved varieties, it is becoming increasingly necessary to adopt some scheme by means of which the farmer is assured of obtaining seed of guaranteed genuineness to name.

Important Points.—The size, the freedom from weed seeds, the germination and germinative energy of the seed used throughout the country are important properties; but it must be realized that, other things being equal, it is the *breed* of the seed which determines the yield, quality and ultimately the commercial value of the resulting crop. Without a good germination the most prolific variety will fail to produce a remunerative crop, but without an inherited capacity to yield grain of good quality the best germinating seed may yield equally unsatisfactory results.

It will thus be seen that with cereals we are rapidly approaching a stage similar to that already reached with farm live stock. The value of a bull or of a cock cannot always be determined by his conformation: it rests also on the qualities known to have existed in his ancestors, and ultimately ascertained to be present in his progeny.

For this reason the value of a bull of a milking strain is judged by the milk yield of his dam and his daughters; that of a cock by the egg-laying capacity of his mother and daughters. In like manner the entire value of a sample of seed of a given variety must not be judged by its appearance, but rather by the ascertained capabilities of the variety to produce high yield and good quality of grain.

Apart from the economic consideration involved, the Danish root experiments afford evidence of what may be accomplished with cross-fertilizing—as distinct from the more easily managed self-fertilizing—crops. In the different root crops, as in cereals, etc., there is definite proof of the existence of distinct differences in quality and yield both as between varieties and as between strains of the same variety. Thus we arrive at a stage when owing to the botanical likeness of strains and varieties it is impossible to distinguish between them by these means only. Many attempts have been made from time to time to correlate definite botanical characters with equally distinct properties of yield and quality, and even with so clearly a definite feature as earliness in ripening: unfortunately none of these has proved satisfactory when applied, as it must be in practice, to closely related varieties.

In root crops, in deciding comparative values, we rely on the determinations of the important food constituents of the crop: in mangolds and swedes, for instance, this is a question of dry matter, and in sugar-beet, of sugar. The gross yield of a crop may mean very little economically unless it is supplemented with quantitative determinations of this character.

To obtain, the greatest national benefit from crop improvement, especially in cross-fertilizing crops with the

ever-present possibility of the pollen from inferior sorts fertilizing superior sorts, the establishment of those varieties, or strains of varieties, with the highest values should imply the elimination from cultivation of those with low values. In Denmark this was brought about voluntarily; the pressure of results of comparative trials carefully and perseveringly collected and published for a series of years, first by a body organized by farmers themselves and latterly by a Committee nominated by the State, was sufficient to divert the attention of cultivators from the producers of inferior seed to others offering seed of proved superior varieties and strains. In India, when dealing with improved varieties of cotton, it was found necessary, in order to prevent the cross-fertilization of superior with inferior varieties, to obtain statutory authority to prohibit compulsorily the cultivation of inferior sorts in, and adjoining, areas where the improved varieties were under propagation.

Value of Breed or Strain.—There is little necessity to add to the existing measures that have been adopted to secure the provision of good seed—that is, seed of good germination and purity—in this country, for the Seeds Acts as well as the Official Seed Testing Stations have made, and are still effecting, a very appreciable improvement in the national seed supply. What is required now is a keener appreciation of real quantitative and qualitative values of the breed or strain of the seed available. At times there is a tendency to attach too great a value to new introductions, on occasions, possibly, under the stimulus of truly remarkable promises by the seedsman, backed by the records of individual non-comparative performances of the new variety. Under these conditions new or improved varieties are circulated throughout the country, and it is some time before they

reach their proper level. Some few succeed and make a permanent impression, others as gradually and as surely die out or are withdrawn from cultivation. This surely represents a happy-go-lucky state of affairs, which is most undesirable. Plant improvement we certainly require, but to flood the market with new varieties, frequently possessing no claim to attention other than their newness, can in no sense be regarded as an improvement. What appears to be required is a rigid comparison of varieties of all crops followed by an elimination of the unfit, and subsequently a restriction of the circulation of new varieties, unless they are shown to exceed the already established and proved varieties in some direction of real economic value. Nothing is likely to retard the ultimate objective of plant breeding, or to reduce the interest of the farmer by confusing the real issue, more than the mere multiplication of varieties, regardless of their economic value in relation to older proved varieties.

It is uneconomic to keep a cow with a poor milk record, a badly thriving bullock, a badly fattening pig, a poor-laying hen, especially when superior animals requiring the expenditure of just the same care, attention and food are available. Although with crops similar varietal differences take a longer time to establish, as they require study through a number of seasons, they are not the less existent and none the less important in the rural economy of the country. If the attainment of comparative values with crops requires the expenditure of more time than is the case with animals, they then demand more immediate action, for in no branch of agricultural activity is it truer that time is money.

The determination of the genuineness to name of

samples of, say, cereals offered for sale is not a matter that can be lightly undertaken, for the differences existing between the grain of some varieties are matters of degree rather than of kind. Nevertheless the subject is one that in the opinion of the authors calls for serious attention by those in charge of the official Seed Testing Stations. Efforts in this direction, although they may for a time be merely tentative, would ultimately focus more attention on the question; and once growers realize the existence of differences in value between pure and impure seeds, a demand for a higher standard of genuineness to name will be created, which seed vendors will be obliged to endeavour to maintain.

In regard to the seeds of varieties of other crops, such as turnips, mangolds and clovers, the position is much the same. The public are not protected either against the extravagant claims of the dealers in new varieties, nor is there any guarantee that varieties of good repute will breed true to name.

CHAPTER VI

IMPROVEMENT OF ANIMALS: GENERAL PRINCIPLES

As was stated in the Introduction, the main object of this book is to illustrate and explain recent advances in the improvement of plants and animals that have been made with the aid of scientific knowledge. In the preceding chapters many instances have been given of the successes achieved by plant breeders. New varieties of wheats, barleys and other crops possessing valuable economic characters have been introduced as the result of the application of scientific knowledge to practical problems.

In regard to animals, however, no such striking catalogue of successes can be made. The improvement of animals is a slow process. In a single generation, often in a few months, a single plant produces a multitude of progeny. Even the most prolific of domestic animals, the pig, breeds slowly in comparison with the plants with which the farmer is familiar. As no scientific advance is possible without experiment, our knowledge of the laws of heredity in animals is advancing slowly, and experiments with animals are not only slow, but also costly.

Before we consider the breeding of animals in greater detail a question must be answered—What evidence have we that the new principles of heredity of which we have spoken apply to the animal?

Unit Characters. — In the forefront of these new principles we have placed the Law of Unit Characters—that is to say, we believe that an individual, whether plant or animal, does not behave in breeding as an individual whole. Characters present in a parent may or may not

appear in all the progeny, and each individual character may behave independently—go its own way, as it were—whatever characters may originally have been associated with it. The progeny of the two parents is not a blend of all the characters of both: each child represents a shuffle, as it were, of a fixed number of cards, in process of which some characters may be left out. If left out of both body and germ cell, there will be no inheritance of a "tendency" to reversion. The inheritance of the Andalusian fowl, to which allusion has already been made, provides an example. Here are the facts. The characteristic colour of the Andalusian fowl is "blue"—that is, a fine pattern of black and white. When two Andalusians are bred together the progeny are not all blue; some are, but there are also chicks which are wholly black and some which are speckled white. As a matter of fact it is found that when large numbers are used, the proportions of the various colours are one black to two blues to one white. Further, if the blacks be inter-bred, the blue of the Andalusian does not reappear. Similarly when the whites are bred together the progeny is always white. On the other hand, if the blues be inter-bred it will be found that black, white and blue appear again in the proportions 1:2:1. From these facts the conclusions are obvious: black and white are unit characters; when both are present the "blue" colour appears; but black and white may also go separate ways in inheritance, and a bird which for example is white contains no black and does not therefore transmit black to its descendants.

In this case, therefore, we have an instance of a principle which, as we have shown, continually operates in the case of plants. The ratios, too, in which the various colours

appear fit exactly with facts that have been observed in countless instances in the case of plants.

Soon after the discovery of Mendel's law, experiments with fowls were carried out by Bateson and Punnett at Cambridge with the object of discovering the principles which regulate the inheritance of comb character in fowls. After breeding some ten thousand birds the experimenters found that the inheritance of certain comb characters is strictly in accordance with Mendelian law.

The normal shape of the comb, as found, for example, in the Leghorn, is "Single." Another shape of comb, found in Wyandottes, is known as "Rose." Single comb and rose comb behave as unit characters. For example, if rose is crossed with single, the first, or F. 1, generation have all rose combs; but if these birds are bred together "single" reappears. This extracted single, however, will breed true to single.[1]

Some examples of characters which have been proved by experiment to behave in inheritance as units are the following:—

(1) Horned and hornless characters as well as black and red colour in cattle are Mendelian pairs.

(2) Comb characters in fowls: in addition to "rose" and single, "pea" (comb) and single are unit characters.

(3) Many coat colours in rabbits have been shown to behave as units. Hair quality known as Angora is also a unit character.

[1] The scientific breeder describes a single-comb fowl as "pure" for single; it may, of course, be anything but pure for other characters. In reading Mendelian literature it should always be remembered that the word "pure" is used in a special sense as meaning pure for the character under consideration only.

(4) Horned and hornless characters in certain breeds of sheep are also subject to the same law.

(5) Similarly, characters in rats, guinea-pigs and other small animals have been proved to be units.

It is apparent, therefore, that there is a considerable mass of evidence which establishes, without room for reasonable doubt, that the principle of unit characters is applicable in *many instances* to inheritance in animals, and further, that these characters obey the Mendelian law in regard to the proportions in which progeny of various constitutions appear in families.

It should, however, be clearly understood that in regard to animals there is no great body of experimental evidence similar to that which exists relating to plants. In particular, it cannot be confidently asserted in the light of existing evidence that the inheritance of certain characters of economic importance is strictly governed by the Mendelian law. These characters are generally of a quantitative nature—that is to say, they are defined in terms of measurements, such as weights either of the animal's body or of some product—such as milk. In this connexion it should be remembered that in the absence of experimental evidence it cannot be assumed that a particular quality is a single Mendelian unit character. In the case of some wheats, for example, it has been shown that the colour of the grain is regulated by a number of unit characters of the same kind. Indeed, it may be admitted that many "qualities" are not subject to the Mendelian law at all. On the other hand, when the history of the improvement of animals is examined there is hardly an advance which cannot be explained on the basis of modern scientific laws of inheritance.

In succeeding chapters we propose to explore that

history, and hope to be able to produce convincing proof of this observation. Before we do so, however, it is necessary to give some account of what is, frankly, a theory, framed to explain a matter which has hitherto been regarded as mysterious, but which in the light of this theory becomes capable of explanation.

Sex.—No theory of inheritance is complete unless it offers an explanation of the phenomenon of sex. It is believed by scientists that the inheritance of sex is a simple case of the Mendelian law, and in this manner. If we suppose that the sperm cells of the male are of two descriptions, one of which is predominately male in character and the other predominately female: if, further, we assume that the ova of the female are all of one kind and thus predominately female, what would happen in the process of reproduction? Clearly the fertilized ovum might be of two kinds: one formed by the union of a sperm of the male type with an ovum of the female type; the other formed by the union of a sperm of the female type with an ovum of the female type. If now we suppose further that *maleness is dominant*, it follows that, as a result of these unions, one (which may be written *mf*) will be male, while the second (*ff*) will be female.

It would be in accordance with observed facts in relation to Mendelian characters generally to find, if the male invariably produces sperms of two kinds, that, on the average, the numbers of each should be equal. The result would then be that the number of males and females should be sensibly equal, and this is, as we know, what happens in nature. The facts, therefore, are in accordance with theory. It should, however, be observed that this hypothesis relates only to the characters that distinguish sex

—mainly the genital organs, their appendages and the functions associated with them. There is nothing to preclude one sex from carrying, recessively, characters which when borne externally are distinctive marks of the other sex. The constitution of a bull as regards sex being *mf*, he may carry the milking (and other) capacities of his mother; for the *f* determinant which goes into one half of his sperms came originally from his dam. In fact we know definitely that in certain cases of disease and malformation in human beings (colour-blindness for example) one sex may carry recessively a condition which appears in its offspring of the opposite sex only.

For the sake of simplicity it has been assumed so far that the hybrid character in regard to sex exists in the male only. This is not true in regard to all animals, but it is so in the case of mammals. In birds the position is reversed: the female bird produces ova of two kinds in equal numbers, of which one is male determining, the other female determining. The male bird produces sperms of the male-determining type only, and femaleness is dominant over maleness. When, in birds, a female determinant unites with a male determinant, the result is a female; but when an ovum of the male type meets a sperm of the male type the resulting individual is a male. The hen bird has the constitution *fm*, the cock is *mm*; and it should be noted that *ff* cannot be produced, while *fm* and *mm* are produced in equal numbers. On the other hand, in mammals *mf* and *ff* are apparent as male and female respectively; *mm* does not exist. It would not have been necessary to venture on a statement of this somewhat recondite theory if it were not the fact that recently it has excited much attention in

relation to poultry breeding, and in a less degree in regard to breeding for milk.

Self-fertilization, Segregation, In-breeding.—It has been said that the application of scientific principles to animal breeding presents particular difficulties. The separation of the sexes is perhaps the source of greatest difficulty. In the chapters dealing with plant breeding the reader will have noticed that the practical plant breeder makes great use of self-fertilization. After the first cross has been made—that is, when the F. 1 generation has been obtained—the plant breeder's next step is to self-fertilize the F. 1 plants. This he does in order to secure a complete reshuffling—the technical term is segregation—of the unit characters. He expects that if he secures a large enough F. 2 generation, somewhere among it he will find an individual—or individuals—containing the new combination of characters which he seeks. This process of self-fertilization is, naturally, impossible in the case of animals. The nearest approach to it is secured by resorting to "in-and-in" breeding. This form of breeding falls far short of self-fertilization. When that is practised, the male and female elements which unite to form a new individual come from *one* individual—the genetic composition is identical. In the case of the in-and-in breeding of animals, on the other hand, the chances are that the two parents, however closely related, are not precisely similar in germinal constitution; complete segregation may, therefore, not occur. Besides, when it does occur, the result often is to bring out certain undesirable characters affecting the vigour of the offspring. Practical breeders recognize that in-breeding is attended with dangers. Some scientists go the length of saying that in-breeding *in itself* is not dangerous; it may, they say, bring

latent defects to light, but at the same time, and in a similar manner, it may strengthen desirable characters. Experimental evidence in support of this view can be quoted. An investigator in America had in-bred white rats for upwards of twenty-five generations and, at the end, his stock was as healthy and vigorous as the original animals; but, as a business consideration, caution must be observed, for no extensive experiments on prolonged in-breeding have been made with larger animals. When we come to consider the case of cattle and sheep, the matter will be discussed in greater detail.

CHAPTER VII

BREEDING OF DOMESTIC ANIMALS

We may now briefly review the history of improvement of a number of breeds of domestic animals, and consider in the case of each of the principal varieties (1) whether the new knowledge throws any light on the methods employed in the past in improving the various breeds, and (2) to what extent that knowledge is likely to help in solving the problems relating to improvement which still confront the practical breeder. It has been said already that the scientific breeder cannot, like the plant breeder, point to notable successes already achieved. He may, however, with confidence express the conviction that a knowledge of the laws of heredity, so far as these have been ascertained and applied, should form an essential part of the equipment of the practical breeder, substituting as it does definitely ascertained principles for knowledge, which, however useful in the past, in the light of modern conditions is now outworn.

Cattle.—It is universally admitted that the British breeds of beef cattle are unsurpassed. Britain has been the stud farm of the world. During the last century, as each new country was opened up, recourse was had to this country for its stock cattle. The British Shorthorn, Polled Angus and Hereford breeds occupy the whole of the American continent, Australia, New Zealand and to a large extent South Africa. It will be of interest, therefore, to trace the beginnings of skilled cattle breeding in this country, and endeavour to discover how far the methods employed by the early pioneers are in consonance with modern views on breeding. If, as we hope to show,

these early successes were achieved as the result of applying to the practical problems of stock breeding principles, which, although the early practitioners may not have formulated them as laws, were such as modern scientific knowledge would commend, it may fairly be argued that these laws cannot be regarded as merely "theory"; they must be put in the same rank as facts.

There is no need to enter on the controversial field of the origin of British breeds of cattle. It is clear that in the course of centuries (the Romans, no doubt, had a share in the business) blood from many sources was introduced. For the purposes we have in view it is not necessary to go farther back than the early part of the eighteenth century: further, we may confine our attention to the northern portion of England, for it is in these counties—Durham, Yorkshire, Leicester and Derbyshire—that improvement really had its birth.

During the early part of the eighteenth century the practice of agriculture underwent a great change. So far as live stock are concerned, the dominating feature of agriculture up to 1700 or thereabouts was that the system of husbandry then practised did not provide winter keep for live stock. Cattle not required for milk or for labour during the winter were killed and their flesh was salted for winter use. The cow was valued for its milk as now, but the bullock was, primarily, a beast of labour and, secondarily, a source of food; the horse was bred for the serious business of war.

Turnip husbandry altered matters: the provision of winter keep became an integral part of good husbandry, and it followed, naturally, that attention should be given to improving the then existing breeds of cattle. Contem-

porary records and traditions establish that at or about that time the indigenous breeds of cattle in Britain were very varied in body shape, quality of flesh, colour and, in a less degree, capacity for milk production, though there is evidence that, as early as the middle of the preceding century, heavy-milking cows from the Low Countries had been imported in considerable numbers, so that Continental blood had been introduced before improvement began. To some degree, no doubt, the various breeds were adapted to the part of the country in which they were kept, but systematic improvement was nowhere practised. At any rate no one had pursued a definite plan of improvement.

The history of improvement began with the famous Bakewell of Dishley, and, whatever may be thought of his methods, the outstanding fact remains that he set about to improve the Longhorn systematically: he had a theory of improvement which he put into practice. Bakewell was born in 1726 at Dishley, in the county of Leicester, and for many years was the tenant of the Grange Farm near Loughborough. It is known that he travelled much and brought home animals of the best stock from many of the places which he visited, and used them in his breeding operations. Bakewell's ideas, the theory by which he was guided, may be summarized as follows:—

(1) Like begets like.
(2) Form is related to function: small bone and barrel-like form mean large proportion of flesh and low proportion of offal.
(3) Quality of meat is dependent on breed, not on size or feeding.
(4) Early maturity can be secured by breeding.
(5) Animals whose character it is wished to preserve should be mated without regard to relationship—the practice of in-and-in breeding.

These principles, be it noted, were applied with success to sheep and Shire horses, as well as to cattle.

It must not be thought that these theories of Bakewell's were derived merely from his imagination; they were based, as all scientific theory should be, on facts of observation. He was an ardent experimenter, and in the case of quality of flesh, and proportion of offal in particular, put his theories to the test of practice.

A famous writer on agriculture, Marshall, who flourished about 1780, says in his *Agricultural Survey of the Midland Counties*:

> Thus it appears, that the Midland breeders rest everything on BREED; under a conviction, that the beauty and utility of form, the quality of the flesh, and its propensity to fatness, are, in the offspring, the natural consequence of similar qualities in the parents. And, what is extremely interesting, it is evident from observation, that these four qualities are compatible; being frequently found united, in a remarkable manner, in the same individuals.
>
> Without admitting, or endeavouring to confute, in this place, that the four qualities, here explained, are the only ones necessary to the perfection of the several species of live stock now under review, we pass on the MEANS, whereby those principles have been applied, in attaining the degree of perfection, which is observable, at present, in the district under survey.
>
> The MEANS of IMPROVEMENT, in the established practice of the kingdom at large, are those of selecting females, from the native flock of the country, and CROSSING with the male of an alien breed; under an opinion, which has been universally received, that continuing to breed from the same line of parentage tends to weaken the breed.
>
> Rooted, however, as this opinion has been, and universally as that practice has prevailed, there is little doubt of the fact, that the superior breeds of stock, in this district, have been raised, by a practice directly contrary; namely, that of breeding, not from the same line, only, but the same family: a practice which has now

been so long established, as to have acquired a technical phrase to express it: "BREEDING IN-AND-IN" is as familiar in the conversation of Midland breeders, as CROSSING is in that of other districts. The sire and the daughter, the son and the mother, the brother and the sister, are, in the ordinary practice of superior breeders, now permitted to improve their own kind; and through the assistance of this practice, as will appear, the bold leader of these improvements produced his celebrated stock.

The argument held out, in its favour, is that there can be only one best breed; and if this be crossed, it must necessarily be with an inferior breed, the necessary consequence of which must be an adulteration, not an improvement.

How far this novel practice may, in a general light, be considered as superiorly eligible would be improper to be discussed, in this place; in which I mean to convey, only a general idea of the present practice of the district; in order to save repetition, and to enable the reader to follow me through the several parts of the enquiry, with greater facility. To this intent, it must likewise be understood, that, although much has probably been done, by BREEDING IN-AND-IN, much also has been done, by CROSSING; not, however, by a mixture of alien breeds, but by uniting the superior branches of the same breed.

The degree of excellency obtained, however, through these means, is not more remarkable, than the rapidity with which the improvement of the several breeds has been carried on, and extended; not over this district, only, but to various parts of the island.

As evidence of the extent to which Bakewell resorted to in-and-in breeding another quotation from the same author may be added :

Mr BAKEWELL is in possession of many valuable individuals, males and females. His bull D., generally known by the name of the "mad bull," is a fine animal, and is a striking proof of the vulgar error that breeding in-and-in, weakens the breed. He was got by a son of Twopenny, out of a daughter and sister of the same celebrated bull; she being the produce of his own dam. Nevertheless, D. is the sire of Shakespear, by another daughter of

the same bull, and is probably the most robust individual of the longhorned breed; while D. himself, at the age of twelve or thirteen years, is more active, and higher mettled, than bulls in general are, at three or four year old.

This has long been considered as Mr Bakewell's best bull; and has been kept, principally, for his own use. He was never let, except part of a season to Mr. Fowler; but has had individual cows brought to him, at five guineas a cow.

Mr Fowler's cattle are, at present, in the highest repute. His cows have long been considered as of the first quality:—of the best Canley blood. And his bull Shakespear, already mentioned, has raised them to a degree of perfection, which, in the opinion of the first judges, the breed of cattle under notice never before attained.

This extraordinary animal is now (1789) eleven years old, and firm in his constitution; but so lame in his hind quarters, as to render him at present, and during the last season, entirely useless.

The breed improved by Bakewell—the Longhorn—eventually went down in competition with the Shorthorn; but there can be no question that Bakewell and his methods were successful, and made, as the quotations from Marshall show, a profound impression on his contemporaries.

He was visited by the most prominent agriculturists from all countries with the avowed object of studying and adopting his methods. Amongst others came the famous brothers Colling, justly regarded as the founders of the modern Shorthorns. Here is what a leading authority [1] on breeds of cattle says on this subject:

But the greatest argument for the Bakewellian system is that the breeds that superseded the Longhorn were originated in the same manner. Besides, to say nothing of his horses, the blood of Bakewell's Leicester sheep, which were equally or more inbred

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[1] *The Evolution of British Cattle*: James Wilson, M.A., B.Sc. Vinton & Company.

than his cattle, now flows in the veins of every long-woolled sheep that trots. . . . At the present day there are no Shorthorns which are not descended from Charles Colling's Comet. . . . There again we have a breeder who, like Bakewell, started with the best stock he could find, and by in-breeding eliminated the chances of uncertainty in their progeny; and the system, much modified, has been adopted by the leading Shorthorn breeders down to the present day.

We have seen that in the eyes of his contemporaries Bakewell's greatest advance seems to have been the extent to which he practised "in-and-in" breeding.

This he did in pursuit of the principles "like begets like" and "put the best to the best." In fact, however, he adopted systematically another principle which, as we have shown in the introductory chapter, is at the root of modern scientific breeding. He applied the test of performance to his sires: for his purposes the best was the animal which, in addition to possessing good qualities of its own, proved capable on test of transmitting these qualities to its offspring. For this purpose he made a practice of letting out sires on hire to his neighbours, and, since the animals were his own property, he could bring back to his flocks and herds those sires which, after test, had proved themselves to be "prepotent." As we have said, Bakewell's methods with the Longhorns were copied by the famous brothers Colling in establishing the breed of Shorthorns.

In the case of another famous breed—the Polled Angus—there is the same story to tell. The crossing of breeds of diverse types in order to get a certain combination of characters — "hornlessness, a stout body, round rump, short legs and black colour"[1]—was followed by intense

[1] *The Breeding and Feeding of Farm Stock*, p. 28: James Wilson.

in-breeding to fix the type. "The Bakewell of the North East of Scotland was Hugh Watson of Keillor in Forfarshire. . . . While Watson was still young he visited Robert Colling. He may not have decided then to adopt in-breeding, but he did adopt it by keeping a son of a bull bought at Brechin for his next stock bull and persisted in it, by having every stock bull for the remaining fifty years of his lifetime succeeded by one or other of his sons. Watson's method, like Bakewell's, was to select his best young animals for stock bulls and retain those that proved good stock-getters till they were no longer useful." [1]

Space will not permit of a detailed examination of the history of other breeds of cattle. Briefly, it is the same story in every case: improvement dates from the adoption of Bakewell's methods—the crossing of indigenous types with others, in-breeding to fix the type, and finally, the rejection of animals which failed on test to breed "true" to the type desired.

Breeding for Milk.—We must now consider, briefly, a subject which has come into prominence in recent years—Breeding for Milk. For a century at least the efforts of stock improvers were directed mainly to breeding for beef—that is, to combining in one animal such qualities as low proportion of offal, quality of "joint" (in the butcher's sense), and early maturity. Except, possibly, in the case of the Ayrshire and Channel Island breeds, milking capacity with early improvers was a secondary consideration, and, incidentally, it may be noticed that the Channel Island breeds provide one of the best examples of the success of in-breeding. For upwards of a century these breeds have been in-bred, for not a single outcross of other

[1] Wilson, *loc. cit.*, p. 29.

breeds has been permitted during these years within the few square miles that these islands comprise.

In regard to this matter we must venture what will be regarded as a controversial statement. In breeding for milk the British breeder may be said to have ceased to maintain pre-eminence; he has, in common opinion, been outstripped by Continental and American breeders. One need only recall the phenomenal prices realized at a certain sale of imported cattle a few years ago to be convinced that, in the main, this statement is true.

It may well be that, in some respects, the foreign strains are not entirely well-suited to the special conditions of this country, as their beef qualities are below British standards; but in regard to both heavy milking and *the capacity of transmitting that capacity to offspring* there can be no reasonable doubt that certain essentially foreign breeds are superior. On this assumption, therefore, is there anything special in foreign practice to which this superiority can be ascribed? There appear to be two such special features: (1) the more general adoption of milk-recording; (2) the greater importance attached to the progeny test of the sire; and be it noted the one is complementary to the other. If we are to appraise our sires on the basis of the performance of their daughters, we must have accurate records of the performance of these daughters.

As we are far behind certain foreign countries in the extent to which milk-recording is practised, it follows that we are falling behind in the equally important matter of breeding for milk.

We may be permitted to offer some observations on the scientific aspect of this matter—not as conclusions, but

rather as a possibly useful contribution to the knowledge that practical men already possess on the matter.

Beef and Milk in the same Breed.—First, as to the possible combination of beef and milk in the same breed. In the absence of experimental evidence we cannot assume, as some scientific writers unfortunately have done, that these characters are Mendelian: they are certainly not single unit characters, but it may be worth considering whether they may not be the result of the interaction of a number of unit characters either of the same description (such as those which produce the red colour of wheat grain) or of dissimilar character, such as those which produce the heavy "yielding" capacity of the cereal plants.

If, then, beef and milk are the result of the interaction of a number of unit characters, there is no reason why it should not be possible to combine the two. By common agreement the efforts of upwards of a century have resulted in the production of the unsurpassed beef breeds of this country. This has been achieved by simple methods of breeding and selection, with, however, one main outlook —beef. If the selection had been extended to milk the process of improvement—that is, from an abstract scientific viewpoint—would have taken longer, that is all. In support of this conclusion we may point to the success that has already been obtained in building up a strain of milking Shorthorns. If progress is to be made in breeding for milk, we venture to think that practical breeders should adventure; they should not be discouraged by statements—which are not based on experimental evidence —that there is any fundamental incompatibility between beef and milk.

At the outset, however, a formidable difficulty must be considered. In breeding for beef the characters which have been so successfully fixed show themselves in both sexes; milking capacity shows itself in the female only. It is difficult, therefore, to follow Bakewell's fundamental principle of "putting the best to the best." A bull naturally can give no direct evidence of possessing—much less of power of transmitting to his daughters—milking capacity. That he can influence milking capacity is now admitted by all practical men. Scientifically, there is of course no possible doubt about it. We say nothing as to milking "points" in a sire. There are certain bodily characters which many practical men believe indicate milk. They may be trustworthy indications: the scientist does not deny the possibility that they are, but, from his standpoint, there is no satisfactory evidence either way; he must hold the question in suspense. In these circumstances, what should the practical man do? The answer is that he should judge the sire on the basis of performance—that is to say, on the milk yield of his daughters. If he will do so, he will merely be practising Bakewell's methods, and, as we have shown, all the leading breeds of beef cattle in this country owe their present excellence to the adoption sooner or later of these methods.

For Bakewell the best sire was the best getter of progeny like himself. In terms of milk the best sire is the one which gets daughters having a yielding capacity as good as or better than that, shall we say, of their dams, or that of the sire's female ancestors—*i.e.* who justifies his pedigree by his performance.

"Sex-linkage" and Milking Capacity.—Lastly, there is one other scientific aspect of the matter that must be

considered. It is sometimes suggested that the inheritance of milking capacity is "sex-linked." The reader will remember that scientists believe that sex is a Mendelian unit character. In the case of mammals it is believed that the male produces an equal number of sperms of two descriptions and that the ova of the female are all of one kind: the union of two dissimilar germs produces a male; the union of two germs of the same kind result in a female.

When, as sometimes happens, another unit character—it may be colour or liability to a certain disease (as colour-blindness, or hæmophilia [1] in man)—is "linked" to sex, we get sex-linked inheritance: the character in question, in certain matings, is transmitted to offspring of the other sex only. What would this "theory" mean in relation to the inheritance of milk? It would imply that a special capacity for deep milking would be transmitted to the male offspring only of a deep milking cow, and that they, in their turn, would transmit it to *their daughters.*

For the practical breeder this theory has this lesson. In the absence of experimental evidence the suggested happening is merely a not unlikely possibility; satisfactory evidence for or against is lacking, and, that being so, it is all the more needful (1) to judge a milking bull on the performance of his daughters; and (2) to have particular regard to the performance—as judged by progeny—*of the sons* of a deep milking cow.

In short, there is every reason, both practical and scientific, to pay particular regard to the performance of the daughters of the milking bull as providing the best chances of practical success in breeding for milk.

In this connexion it should be noted that the Ministry

[1] The popular expression for sufferers is "bleeders."

of Agriculture has recently instituted a Register which is intended to provide practical breeders with information of the nature indicated. Registers of this description have been in use in America for some years, and have proved of the utmost value to the industry.

There is, of course, one great obstacle to progress in breeding for milk, and that is the general practice of slaughtering a herd bull soon after his daughters reach maturity. In a subsequent chapter the arguments for and against in-breeding will be considered. It will be sufficient here to say that on a review of history, and giving due weight to experimental evidence now available, the risks, such as they may be, are worth taking. As to the alleged practical difficulties of keeping an old bull, they are not serious. If, however, the merits of a sire as a getter of milking stock are recognized only after his death, it is suggested that a son and daughter of his should be mated on the chance that their father's valuable qualities may thus be perpetuated.

Further Improvement of Beef Cattle.—The question may be put : What view does the scientist take as to the possibility of further improvement in beef cattle ? The following suggestions may be made. Something may still be done in the direction of improving constitutional qualities. Earliness of maturity was one of the characters which Bakewell set out to improve. He and his successors, working on similar lines, were largely successful, and in quite recent years we know that as a farther step the production of "baby" beef has become possible. There remains, however, great variation between individuals in regard to capacity for fattening. Some animals are capable of making better use of food-stuffs than others : some are

"doers." It may be that some of these differences would disappear if our scientific knowledge of feeding was more precise, but the possibility of improvement in this direction by breeding and selection is worth exploring.

In this connexion it may be interesting to give a figure which has been derived from the study of a large number of feeding trials. It is even betting that in the ordinary winter period the weight put on by one beast will be within 13 per cent. of the figure obtained by taking the average of a large number of beasts. The magnitude of this figure suggests that the variation may be due to differences of "strain" and consequently capable of elimination by selective breeding.

Further, on this matter of feeding it may be observed that, with the ever-increasing cost of imported foods, the returns for the expense involved in the rearing of animals tend to diminish. It is therefore most important that breeders should seek to improve existing breeds of cattle, not only in new directions, but also in respect of qualities in which some degree of excellence already exists. In the case of the dairy cow the means lie at hand—greater attention to the performance of the sire; in regard to beef production, the immediate object should be to level up the standard of performance so as to reduce the proportion of uneconomic beasts—that is to say, animals which fail to give an adequate return for the cost of feeding.

CHAPTER VIII

BREEDING OF DOMESTIC ANIMALS—*cont.*

Horses.—We have placed horses after cattle because, in regard to improvement, speed, the quality sought after, and the one in which the success attained has been most remarkable, is an aspect of the matter in which, primarily, the farmer is not interested. Further, it seems highly probable that "speed," or more accurately, perhaps, the capacity for winning races, is subject, more than is the case with any other economic character, to what the scientist calls environmental or incalculable influences. Still, the history of improvement of the race-horse, and also of such types as the Shire and Clydesdale, goes to confirm the truth of what we have ventured to describe as the laws of inheritance. We have, again, the crossing of diverse existing types, followed by in-breeding, combined with breeding on the basis of records of performance. In relation to race-horses, however, history shows that there is an extraordinary divergence between pedigree and performance.

The development of the race-horse—the thoroughbred—may be said to have begun with the purchase by our first Stuart king in 1616 of "Markham's Arabian." Subsequently Eastern horses seem to have been freely used down to the end of the eighteenth century. It was from the reshuffling of characters which resulted from the introduction of Eastern blood that the thoroughbred, as we know it to-day, has been produced. Other types of horses, such as the Shire, Clydesdale, Cleveland Bay and others, are believed to be the improved descendants of the great war-horse of the Middle Ages, itself a composite product;

but there is no evidence that the improvement of these breeds has ever been undertaken in the systematic manner introduced by Bakewell. It is probably for this reason that these classes rarely breed true in the Mendelian sense.

It so happens, however, that in regard to certain colours in horses it has been shown conclusively that the Mendelian law applies. Bay and chestnut behave as a complementary pair of Mendelian characters. The truth of this assertion can easily be tested by anyone who cares to check breed records, by noting that chestnut bred to chestnut invariably gives chestnut, whereas bay bred to chestnut gives either bay or chestnut, bay being dominant to chestnut. There are consequently two descriptions of bay, one "pure" for bay, and the other bay carrying chestnut recessively.

The improvement of the horse has undoubtedly been hindered by the belief—and results would appear to support it—that the best horse for certain purposes is obtained by crossing. The hunter and the "light horse" continue to be bred in this way. The results are notoriously uncertain, and, as might be expected on theoretical grounds, the offspring from such stock interbred is still more variable. The schemes for the improvement of the horse promoted by the various Governments have, no doubt, done some good, but their efficiency is limited to some extent by the degree in which the State has taken a direct interest in the subject. There can be little doubt that much good has been done in those foreign countries in which the State directly controls horse-breeding operations and maintains Government Stud Farms for experimental work.

Sheep.—When the history of the improvement of sheep is examined, the name of Bakewell recurs. The famous

Dishley breed of Leicester was created by him, and by the methods with which we have dealt at some length in connexion with cattle. It was in improving this breed of sheep that he practised most intensively his system of testing his sires by hiring them out for a season. His success financially may be estimated from the fact that whereas in 1760 he obtained only a few shillings for the hire of a ram, ten years later his famous ram "Two Pounder" was rented for the equivalent of 1200 guineas a season. In view of these figures it is difficult to realize that at an early stage in his career Bakewell was saved from bankruptcy by the gift of a large sum of money raised by public subscription. Eventually his affairs righted themselves entirely.

Not long after Bakewell there appeared another celebrated pioneer, Robert Ellman of Glynde, the founder of the improved Southdown. His methods also were based upon Bakewell's. He converted the old Sussex sheep, an animal with "light fore-quarters, narrow chest and long limbs," into the typically compact Southdown of to-day; the wool character, it should be noted, being little altered in the process: in other words, wool character in the Southdown proved to be dependent upon characters separable from others in selective breeding. In fact, the history of the various breeds of sheep discloses that little has ever been achieved in improving wool character by ordinary breeding methods. Black hair and kemp still continue to trouble sheep breeders, particularly in the case of mountain breeds, such as the Welsh Mountain and Scotch Blackface—in which constitutional qualities are of such supreme value that wool improvement has received little attention.

Some years ago an attempt was made at Cambridge to investigate the laws of inheritance of wool character. It may be of interest to give some account of this experiment, for it provides a striking illustration of the difficulties, both scientific and practical, with which breeding experiments with animals are surrounded. Two Merino rams were imported from Australia. They were put to a number of Shropshire ewes. The first (F.1) generation consisted of upwards of fifty animals, all showing a considerable degree of uniformity in wool character. It will be recalled that in connexion with the breeding of plants it was explained that in order to shuffle and recombine diverse characters it is necessary to interbreed the F.1 generation. Back-crossing to the parent breed would not have produced anything fundamentally new, such as Shropshire body character combined with a Merino fleece. It may not, of course, be possible to produce such a novel combination as this, but if it is at all possible to do so, *it can be achieved only by persistent inter-crossing of animals of the first cross.* This was done, and the result was in accordance with expectation.

The second interbred generation (F.2) contained sheep showing many recombinations of wool and mutton characters, most of them being "wasters" from every point of view. Yet it could not be assumed that even among upwards of two hundred animals *all* the new combinations had been made, so that it was necessary to continue to interbreed these mongrels. Practical difficulties soon supervened. The resources of the University farm were strained in dealing with the number of uncastrated rams that the conditions of the experiment demanded. The Merino blood introduced a large degree of foot trouble, for the breed seems to thrive on free range only; it cannot be

folded. Then a susceptibility to a parasitic disease developed, with the result that the land became heavily infected with the ova of the pest; further, it was found that the wool characters of sheep infected with the parasite became abnormal, so that it became impracticable to judge whether the characters observed were natural or merely accidental. Finally, the outbreak of war brought the investigation to a conclusion.

This experiment would not have been undertaken had it not been that a previous experiment in sheep breeding was successful. As a result of interbreeding first crosses between a Dorset ram and a Suffolk ewe it was shown that it was possible to transfer the hornlessness of the Suffolk to the Dorset breed—that is to say, sheep were produced with all the characteristics of the Dorset breed except that they had no horns.

It has been said that one of the prominent defects in existing breeds of sheep is the presence, in a varying degree in animals of the same breed, of kemp and black hair. In addition to these obvious irregularities, we are told by wool experts that there is much variation in what may be termed textile characteristics, which can be appreciated by the expert wool-sorter only, and yet affect the value of the wool for industrial purposes. How far these variations are genetic and how far environmental has not been determined. In the Cambridge experiment it was found that the presence of a parasitic worm affected the character of the wool, and practical men assert that the wool of some breeds of sheep reared in certain counties is superior to that of sheep reared elsewhere. It is stated that in New Zealand if sheep are taken from one side of the islands to the other the wool character changes. One of the first problems for the

scientist, therefore, is to clear this matter up. Broad differences such as exist between Merino and short wool are certainly genetic, but within this range of characters there are numberless grades, as to which it cannot be affirmed with certainty whether they are genetic (and therefore fixable) or not. At the present moment investigations into the inheritance of kemp are going on in Wales in association with the University College, Bangor. There are already indications that the presence of kemp is to some extent genetic—that is, hereditary.

With regard to Merino wool, it has been asserted that British wools could be improved if some of the Merino characteristics could be imparted to them. With the object of testing this hypothesis, in 1924, under the auspices of Professor Barker of the University of Leeds, a number of Merino rams were imported from Peru (where an extremely hardy strain of the breed has been established many years), and these are being crossed with various British breeds. Incidentally, it may be noticed that at Ross, in Hereford, a flock of pure-bred Merinos has been maintained for nearly a century, so that there is apparently no climatic reason why the breed should not flourish in this country. Unfortunately the mutton is of poor quality, and the constitution of the breed is such that it does not take kindly to folding. The scientific breeder's problem in regard to Merinos is to determine how far the wool and mutton characters are separable, and whether the former can be developed on a sheep suited to the economic conditions of the sheep industry in Britain.

It is generally agreed that one of the lines upon which the general improvement of the sheep might proceed would be to reduce the number of existing breeds. These number

approximately thirty, and it is difficult to believe that for practical purposes so many are really required.

Some reference should be made to the island breeds—the Shetland and the Soya: both have a wool of a special quality much sought after by the woollen industries. Here again we are faced with the difficulty of determining how far these special wool characters are genetic and separable (in a Mendelian sense) from mutton and constitutional characters. Such problems cannot be settled until breeding experiments on an extensive scale—costly, and extending over a long period of time—have been carried out. We may repeat that for this purpose the accepted practical methods are useless. These almost invariably proceed on the theory that the desired end can be gained by the breeding of first crosses to one or other of the parent breeds. This was not Bakewell's method; that was an outcross followed by in-and-in breeding and selection.

In the past every attempt to improve British wools seems to have been followed by deterioration in mutton quality—the most valuable characteristic, from a British point of view, the sheep possesses. No progress appears to be possible until scientific investigation has discovered the laws which govern the inheritance of wool characters. It may then become possible to breed a sheep which shall combine superior wool with excellence as a mutton producer.

Pigs.—The early history of the breeds of swine is obscure: suffice it to say that the pedigree pig of to-day is the result of the cross-breeding and selection of centuries, during which the blood of European and Asian (the China pig figures prominently in early literature) varieties has been intermingled. From a scientific and practical point

of view, any inquiry into the matter of origins will prove barren, at least in so far as future improvement is concerned. For this purpose we may assume that all the various characteristics of the original breeds are scattered about as so many cards of the limited pack of which each individual is made up. It may also be safely asserted that of all the domestic animals the pig is the least "pure" in the Mendelian sense—that is to say, if any character is considered, except perhaps colour, the proportion of individuals which will breed *true to that character* is comparatively small. Economic characters in particular, such for example as the bacon pig as contrasted with the porker, have not been fixed, but they differ from animal to animal of the same breed. Internal "points" naturally do not figure in breed characterizations: correct "form" is all-important, and in swine external form does not always indicate—and this is certainly so in regard to bacon—internal qualities. There is no history of the application of Bakewell's principles to swine, and it will be remembered that an essential feature of his work was the correlation of external form with quality of meat by slaughtering experiments. The defect in bacon pigs known as "seedy cut" is an example of an internal defect which cannot always be correlated with external features. Recent work by Marshall and M'Kenzie at Cambridge has shown that "seedy cut" is due to the deposition of colouring matter round the mammary glands of the pig, that the defect is probably hereditary, and that it may be transmitted independently of general skin or hair pigmentation. It is therefore curable by scientific breeding.

In regard to a subject of topical interest—the production of the bacon pig—the following observations may

be ventured. The points of the bacon pig, both external and internal, are well known, but the latter are naturally of more vital importance to the bacon-curer than to the farmer. An animal, or a particular breed of swine, that is not suitable for bacon may command a good price as a porker. The economic aim is, therefore, confused. Where, as in Denmark, the pig breeder has only one interest—the production of a bacon pig for the English market—the way to improvement is clear, and in that country has taken the form of co-operation between the pig-producers and the bacon-curers. The State, too, has taken a hand; for by instituting a scheme of legal grading, coupled with inspection, control is exercised over the breeding stock so as to ensure that animals whose progeny fail to produce pigs of the standard which the curer requires are eliminated. Progress in the direction of breeding for bacon in this country would seem, therefore, to depend primarily on organization, of which a leading feature should be linking-up of the curing industry with the breed societies, with a view to greater prominence being given to bacon points in the judging standard which the latter shall adopt.

Much has been said as to the relative suitability of various breeds and crosses of these breeds for bacon production. The fallacy of much of these discussions lies in the fact to which attention has been drawn above. None of the existing breeds is ideally "pure" for economic qualities. The existing judging standards aim at producing a body form, which for all we know is mainly æsthetic; at any rate they have not been submitted to the judgment of the bacon-curers. From a scientific point of view, there is no reason why a pedigree bacon strain should not be

built up within each of the leading breeds just as a pedigree milking strain has been produced within the Shorthorns.

In the case of swine the Bakewellian methods, particularly the plan of in-breeding, present special difficulties. There can be little doubt that the in-breeding of swine, more than that of any other farm animal, is likely to bring out latent defects, and that this is due to the fact to which allusion is made—viz. the hybrid character (in a scientific sense) of the existing pedigree breeds of swine. None of them breeds true to individual economic qualities. It can only be suggested that, if improvement is to be effected, closer breeding must be adopted ; but whether it would pay any private individual to do so is a doubtful question.

Poultry.—The history of the improvement of poultry from the economic or the "utility" standpoint is comparatively modern. The breeding of fowls for fancy points, on the other hand, has been practised for centuries, particularly in the East, whence the breed originally came. Some of the freak birds produced by the Japanese, for instance the breed in which the tail of the cock bird is many yards long, almost exceed credibility. One result of these activities has been that poultry breeding is a favourite exercise of the geneticist, and numberless instances of the truth of Mendelian laws can be quoted. One reservation, however, must be made : clear instances of the inheritance of quantitative characters—such as fecundity (egg-laying capacity)—are still wanting.

The fowl, however, enjoys the distinction of being the first *animal* for which it was established that the Mendelian laws regulate the inheritance of certain characters ; to scientists it has now the further interest that the phenomenon known as sex-linked inheritance can not only

be demonstrated in poultry in a most convincing manner, but that it has also a useful commercial application to poultry keeping. The meaning of the term "sex-linkage" has been stated in an earlier chapter: the phenomenon to be explained is that in which some particular character can be transmitted to one sex through the intermediary of the other. This may be illustrated by the following case in poultry. Some breeds of poultry have varieties described either as "gold" or "silver." The Brown Leghorn is an example of the former, and the Light Sussex of the latter. When a Brown Leghorn cock is mated with a Light Sussex hen, all the cockerel chicks are silver and all the pullet chicks are gold, and the difference is marked from the moment of hatching. This is a case of sex-linked inheritance: the silver hen transmits silver to her sons only; the silver character is "linked" to maleness.

Now it will be remembered that sex is believed to be regulated by a Mendelian unit character and that, in birds, the female carries maleness recessively, with the result that one half of her eggs bear the female and one half the male determinant; the cock has no influence on sex, for his germs are all of one character only. That this theory of sex is right is confirmed by what happens when the cross is made the other way round. If a Brown Leghorn *hen* is mated with a Light Sussex *cock*, *all* the chicks, both male and female, are silver, and when these silver chicks are bred together *all* the resulting *pullets* are gold. The explanation is rather complicated, and the reader must accept the statement that these facts can be explained only on the assumptions (1) that sex is regulated by one pair of Mendelian factors; (2) that silver and

gold are another pair, of which silver is the dominant, and (3) that silver is "linked" to maleness in such a way that when both silver-bearing and gold-bearing germs are produced by the hen, the silver-bearing go to the male eggs only and the gold-bearing to the female.

The facts described above have an important economic application. To the poultry farmer who specializes in egg-production the rearing of cockerels is generally unprofitable, and in the heavy breeds it is ordinarily impossible to discriminate between the sexes until the birds are two or three months old. By employing the cross between Light Sussex and Brown Leghorn it is possible to market day-old chicks which can be guaranteed to be all pullets. Further, stock birds of high egg-yielding capacity can be used as parents with the knowledge that the first crosses marketed are almost valueless for breeding purposes. The progeny of a first cross show segregation, or, in other words, they are mongrels. The first crosses, on the other hand, unite the virtues of both "pure" parents, and, as first crosses, may show a high vigour. This introduces a phenomenon of breeding that has not hitherto been mentioned—the alleged vigour of the first cross. We shall have more to say on this subject later.

The subject of sex-linkage has been treated rather fully, for the theory has been pursued to some—possibly extreme—lengths in connexion with other breeding problems. It is being asserted that egg-laying capacity is sex-linked and that the high-producing hen transmits her virtues in this respect through her sons only and not her daughters.[1]

[1] In another field it has been suggested that milk-yielding capacity is transmitted through sons only. So far as we know, this is a suggestion only: there is, at any rate, no experimental evidence on the subject.

This gained some currency as the result of certain experimental work done by Pearl at Maine, in America, in the early years of this century. As to this theory, however, it is sufficient to say that Pearl's conclusions have not been confirmed by two subsequent workers on Rhode Island Reds and Wyandottes respectively. At the present moment the hypothesis is being subjected to a rigorous test by Professor Punnett at the Poultry Research Station in Cambridge. Other characters of economic importance in fowls are broodiness, size of egg and colour of shell. As matters stand, brown shell and broodiness—as in Wyandottes—seem to be inseparable; but it has been shown by Professor Punnett experimentally that it may be possible to produce a non-broody bird which lays brown eggs. There is, however, no good evidence that size of egg is a unit character, and that its inheritance is sex-linked.

NOTE

Inheritance in Man.—So much has been said about the Laws of Inheritance and the possible improvements that may be brought about in domestic animals, that it may be permissible—though hardly within the declared scope of this little book—to say something regarding Inheritance in Man. In recent years much has been promulgated in the name of science on the subject of Eugenics—that is, the improvement of man by breeding. If the best authority be sought, it will be found that in relation to man few confident statements can be made. It is true that certain physical characteristics (we have mentioned eye-colour) and such diseases as colour-blindness, hæmophilia and certain malformations are undoubtedly subject to the Mendelian law; but when we come to characteristics of a more indefinite nature—special capacities such as "genius," high musical talent, or, at the other end of the scale, criminal or immoral tendencies—it cannot be affirmed that any "law" is operative. Many such characters are loosely hereditary; they tend, as the expression goes, to run in families, but the point to

be made is that the inheritance is so irregular that no rule of conduct or any regime of State can be advocated, much less imposed by law.

One of the leading authorities on the subject, the late Dr Bateson, F.R.S., addressing the Eugenic Society recently stated that, in his view, there is only *one* hereditary "taint" in regard to which the evidence is sufficiently strong to justify State action. That is the defect known as "feeble-mindedness." This appears to be a definite pathological condition closely related to idiocy, and is characterized by a lack of the normal moral inhibitions. The direct inheritance of this defect is well marked. Many pedigrees have been worked out which establish the fact. The offspring of the feeble-minded, if not idiots, show marked criminal characteristics, particularly addiction to crime of a violent nature, such as murder (generally associated with sexual excesses), robbery with violence, and so on. There is, of course, room for difference of expert opinion on this subject, but the above is the opinion of one who must be regarded as the founder of the science of Genetics.

There is one other matter that may be touched upon. The marriage of relations is often spoken of as dangerous. Modern research in some degree justifies this statement. If a family has shown the presence, in the past, of some form of congenital weakness, the *risk* of its reappearance is probably intensified; but at best it is merely a risk, a probability against which there are generally heavy odds. Unfortunately, too, there is no general agreement as to what should be regarded as a "congenital" weakness from the point of view of inheritance. It is distinctly controversial, for example, whether a tendency to tuberculosis is heritable. In the case of another serious disease—cancer—the evidence negatives the view which is sometimes held as to its hereditary transmission.

CHAPTER IX

IN-BREEDING IN ANIMALS

In the foregoing rapid survey of the history of the improvement of the principal varieties of domestic live stock an attempt has been made to show that there is nothing inconsistent in that history with the laws of heredity so far as they have been ascertained by the modern science of genetics. There is, in fact, much to confirm these laws. It is not asserted that these laws explain the whole matter of inheritance; still less can the claim be made that practical breeders will obtain guidance on every aspect of their business. On the other hand, it must be admitted that this modern science has thrown a flood of light on matters hitherto regarded as mysterious, and has encouraged the hope that by further experimentation greater additions to precise knowledge will be made. Theory is often condemned by practical men: it should never be forgotten that it is to "theory" that we owe most of the advances in practical affairs which make life under modern conditions possible. It was certainly superior scientific knowledge in great part that enabled us in recent years to avert the greatest catastrophe with which a people was ever threatened.

Turning to the business aspect of this matter of improvement of live stock, we cannot fail to be struck by the dominating position occupied by Bakewell and his methods. Here, by the way, was a practical farmer who framed a theory of improvement which he put into practice with, at first, disastrous financial results; but he persevered, was ultimately successful, and lived to see the triumph of his theory and methods all over the country. It may almost

be said that the checks in progress since his time have been due to occasional departures from his gospel. These methods have now, in great measure, won scientific sanction; we say in great measure only because, unfortunately, in regard to a central feature of his system complete scientific knowledge is still lacking.

We have seen that according to the evidence of Marshall, a contemporary, he practised in-and-in breeding to a then unheard-of extent. The prejudice against the practice is universal, and is founded upon a deep-rooted instinct of human nature which should not be lightly disregarded. Man, however, has little regard to the morals of animals and plants, and Nature has less. What has the scientist to say on this matter? In an earlier chapter it has been pointed out that the corresponding phenomenon in plants is self-fertilization, and that the successes of the plant breeder are largely dependent upon the facility with which this operation can be effected in plants. Incidentally, it may be noticed that the cereals have been reproduced by this process since the beginning of time—a fact which justifies the statement that the evils of in-breeding, if any, are not at any rate progressive, otherwise self-fertilized plants would long ago have disappeared off the face of the earth.

What about animals? In the first place, in-breeding is common in Nature. We are familiar with the dominant male who for years at a time reigns over a flock or herd of dependent females. On the other hand, there is no reason to doubt the practical observation that an occasional "outcross" promotes general vigour. Again, therefore, the statement may be made that the alleged evils of in-breeding are not *cumulative*; after a certain point a stationary position is reached. In the next place, in recent

years certain experimental evidence has become available. Scientists in America have made experiments with white rats. After many generations of brother and sister matings (from parents of the same relationship) the final stock was as vigorous as that with which the experiment was begun. In the course of the work, however, some individuals were born defective. These were rejected; the vigorous animals only of each generation were retained. This experiment is now being repeated with sheep at the University College, Bangor, and eventually, it is hoped, it may be extended to cattle.

The American experiment had another interesting outcome. Not only were the final generations vigorous, but they were also uniform in a remarkable degree: so *much so that the stock is now much sought after in many* scientific laboratories which are engaged in research in human physiology and pathology, and for this reason. One animal of this stock varies very little from another in its response to experimental diets. As we all know, feeding experiments with live stock are liable to disclose considerable individual differences in this respect. Every practical man knows the difference between a beast that is a "doer" and one that is not a "doer." Do not these experiments suggest that the existing breeds are genetically different in respect of their capacity for laying on fat? In view of all these facts scientists assert, with some confidence, that inbreeding *in itself* is not harmful; the defects which practical men have observed are merely the result of the "fixing," of appearances on the surface, of defective characters which remain recessive or latent when unrelated animals are mated. The appearance of defective animals is occasional; other members of the family show no evil effects.

In-breeding, as experience shows, is equally effective in fixing good qualities, and this view, it should be noted, fits with the Mendelian "theory" of inheritance. When two individuals carrying, but not showing externally, a recessive character are mated, *some* of the offspring, *not all*, will show this recessive character specially. On the other hand, we must admit that the theory has some difficulty in explaining all the manifestations of the contrasted effect, the *addition* of general *vigour* which out-crossing *sometimes* (not always) produces. This phenomenon is observed even in plants.

Summing up, the practical attitude to this matter may be stated as follows :—

(1) In-breeding is necessary for breed improvement; it fixes type and secures uniformity.

(2) The practical breeder should not be deterred from practising in-breeding by fear of the consequences: if it occasionally results in a waster, it also produces an animal of outstanding merit; more often than not it has no evil consequences on the rest of the progeny. It may be dropped only if *pronounced* sterility declares to an extent that makes the continuation of the procedure unprofitable.

(3) Outcrossing, the introduction of "fresh blood," is justifiable if the object is to produce an animal which shall not be used for breeding purposes, such as a steer for fattening, a fowl for laying only, etc.

Beyond all, it should be persistently borne in mind that the whole history of breed improvement goes to show that, starting with Bakewell, the great improvers all practised in-breeding to an extraordinary degree of

intensity. Bakewell put the best to the best regardless of relationship.

Some authorities pin their faith on "line-breeding," which is simply a less intensive form of in-breeding, and some of the presumed dangers of which it is believed to avoid. Of this system it may merely be said that it is too weak for the believer in in-breeding and too strong for the detractor.

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A SELECTION OF TEXT-BOOKS ON THE SUBJECT OF PLANT AND ANIMAL BREEDING

1. *Mendel's Principles of Heredity*: W. Bateson, F.R.S. Cambridge University Press. (1908, 17s. 6d.) (*Out of print.*)
2. *Mendelism*: R. C. Punnett, F.R.S. Macmillan & Co. (1922, 8s. 6d.)
3. *Heredity in Poultry*: R. C. Punnet, F.R.S. Macmillan & Co. (1923, 10s.)
4. *Heredity in the Light of Recent Research*: L. Doncaster. Cambridge University Press. (1921, 4s.)
5. *Animal Genetics: The Science of Animal Breeding*: F. A. E. Crew. Oliver & Boyd. (1925, 15s.)
6. *Genetics in Relation to Agriculture*: E. B. Babcock and R. E. Clausen: McGraw-Hill Publishing Co. (1918, 20s.)
7. *Inbreeding and Outbreeding*: E. M. East and D. F. Jones. Lippincott Co. (1919, 10s. 6d.)
8. *The Breeding and Feeding of Farm Stock*: James Wilson. Methuen & Co. (1921, 6s.)
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